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COMPARATIVE METABOLISM OF THE CELLS OF VARIOUS CHROMOSOMAL TYPES OF NICOTIANA TABACUM

BY

J. DUFRENOY

INTRODUCTION

MANIFESTATIONS OF LIFE in the cell arise from interactions between cytoplasm and cytoplasmic inclusions as determined by the genetic factors in the chromosomes. The relations between these manifestations of life and the structure of the living matter are evidenced by readjustment of cell materials concomitant with metabolic changes in the cell. The living cell is composed of a few homogeneous materials, each of which can be considered as a "phase," and the living processes take place mainly where these materials come in contact, along "interphases" or "interfaces"; hence the importance of studying the relations of the living materials in the cell without disturbing their interphase relations. Cytology is the science which aims at studying the true nature of each cell constituent, in its normal relation to the other cell constituents, in order to explain the mechanism of cell life.

The structure of living matter.—Each living part of the cell consists of perfectly homogeneous, structureless material, which appears optically empty when studied under the ultra-microscope. Each of these homogeneous materials, representing a phase, has a refractive index of its own. The interphase between two materials differing in their power of refraction may be apparent with ordinary powers of the microscope, especially when oblique illumination is used; when examined under the ultra-microscope, it always appears as a brightly illuminated line between the two dark phases.

General cytological technique.—The living cytoplasm cannot be stained; therefore stained cytoplasm is dead cytoplasm. In cytological technique the death of the cytoplasm must be accomplished quickly enough, through the use of proper killing fluids, to prevent ante-mortem changes from altering its physical structure. Proper killing fluids such as Regaud's, Nemec's, or Meves's kill the cytoplasm, leaving it a mass of very fine ultra-microscopic granules, and preserve the smallest cytoplasmic inclusions as well as the chromosomes. Other killing fluids produce a coarse reticulum and destroy the fine cytoplasmic inclusions.

However, the most delicate and most unstable material in the cell is neither the cytoplasm nor any of its inclusions, but the vacuolar material. Although it is possible, through proper killing methods, to preserve a structure in the cytoplasm which, as seen under the microscope, does not differ grossly from that seen in the living cell, it seems impossible to fix the vacuolar solution. The vacuolar solution, as such, exists only in the living cell, and is flocculated down into a complex of vacuolar precipitates as soon as the cell dies. In fact, the total flocculation of the vacuolar solution may be considered the best criterion of the death of the cell. Life, therefore, seems to depend on certain materials existing in a water-soluble form in the vacuolar solution, and the vacuolar solution has been considered as representing the aqueous phase in the cell, as contrasted with the cytoplasm and its inclusions, the lipid phase.

Cytoplasm seems to be a perfectly homogeneous complex of proteids and lipids, comprising a lipo-proteid wherein neither component, lipid nor proteid, can exhibit its specific microchemical reactions. Any disintegration process, such as arises from increased proteolytic activity, unmasks both components, lipids being liberated into free droplets of oil (giving the microchemical tests for oils) and proteids being precipitated out of the complex or being split into amino acids which may go into solution in the vacuolar sol or eventually crystallize out.

Warburg pointed out that respiration in the cell takes place along the interface, where cytoplasm is in contact with the surface of the vacuolar solution; and H. Devaux and W. D. Harkins suggested that the interface separating two phases is represented by a single layer of oriented molecules. These suggestions should center the attention of cytologists on the surfaces of contact between the cytoplasm and the vacuoles more than on either the cytoplasm or any of its inclusions. In short, no constituent of the cell should be studied apart from the other constituents of the cell, because what is most important is the arrangement of the cell constituents, and their interdependence, as made evident by the microscopic study of their distribution in the cell.

THE RELATION OF CELL METABOLISM TO CHROMOSOMAL CONSTITUTION

METHODS AND MATERIALS

It is generally accepted that the genes control the physiological activity of the plant cell, so that, under specific ecological conditions, any given form of metabolic activity depends upon a definite genetic constitution. Any manifestation of cell metabolism, however, has its material basis within the cell and therefore any change of metabolic activity may be manifested microscopically by a remodeling of the cell structure or, more precisely, by a regrouping of the cell constituents. This indicates the method of attack followed in the present (preliminary) investigation.

We know little as yet about the effect of the presence or absence of particular chromosomes on cell metabolism and on the development and interrelations of cytoplasmic inclusions, mitochondria, or plastids. Allen reports abnormally large plastids in triploid liverworts, and Rhoades recently found that "microspores from normal and male sterile *Zea mays* plants, fixed in Benda's fluid and stained in Heidenhain's iron haematoxylin, showed a profound difference in size, shape, and number of the cytoplasmic elements, which are presumably plastids or plastid primordia."

It was learned by the writer that the *Nicotiana* cultures grown by Professor R. E. Clausen include a unique collection of monosomics, haploids, and triploids of known chromosomal constitutions. From unpublished material, Clausen and Olmo informed me that in pollen of certain monosomic types of *Nicotiana Tabacum* the 23-chromosome grains are easily distinguished from normal grains by the presence of refractive droplets. Dr. Avery observed similar inclusions in some pollen grains.

Researches were therefore undertaken in the Division of Genetics of the University of California with the object of comparing the metabolism of the vegetative and reproductive cells of *Nicotiana Tabacum* affected with chromosomal irregularities with that of normal cells.

VITAL STUDIES OF NORMAL VERSUS DEGENERATING POLLEN GRAINS OF MONOSOMIC N. TABACUM

Staining pollen grains with vital dyes, such as neutral red dissolved in an isotonic solution (Ringer solution, or 7.5 per cent sucrose solution), demonstrates that the evolution of the vacuolar system in abortive grains is inhibited from an early stage. As usually happens in respect of actively enlarging cells, the increase in volume of the normal pollen grain is chiefly caused by swelling of the vacuolar material. Very young normal grains, at the tetrad stage, contain numerous but very small vacuoles in the form of minute droplets. These rapidly enlarge, some of them fusing, so that the pollen grain, when it is ready to be shed, contains a few relatively large vacuoles. The vacuolar solution within each vacuole is stained uniformly by neutral red; but nothing else in the normal pollen grain is stained. The living cytoplasm, within which the vacuoles are imbedded, is unstainable as long as it is living.

In the monosomic type haplo-F or fluted (33146–4), figure 1, some tetrads are made up of one or two good pollen grains, the vacuoles of which can be selectively stained by neutral red, while the remaining pollen grains are stained a dirty red, as a whole, by this reagent. The latter behave as dead cells containing stainable material resulting from the disintegration of the living cytoplasm. Intergradations occur between the normal pollen grains and those which degenerate as early as the tetrad stage, and a definite relation exists between the inability of the vacuoles to develop fully and the failure of the grain to attain normal size and shape. Not only do the vacuoles fail to enlarge in the grains which degenerate, but the solution within them is unstable; it cannot be stained as a whole by neutral red, but is rapidly precipitated in the form of many small granules at the surface of the vacuoles. Such an instability of the vacuolar material is a most common ante-mortem symp-

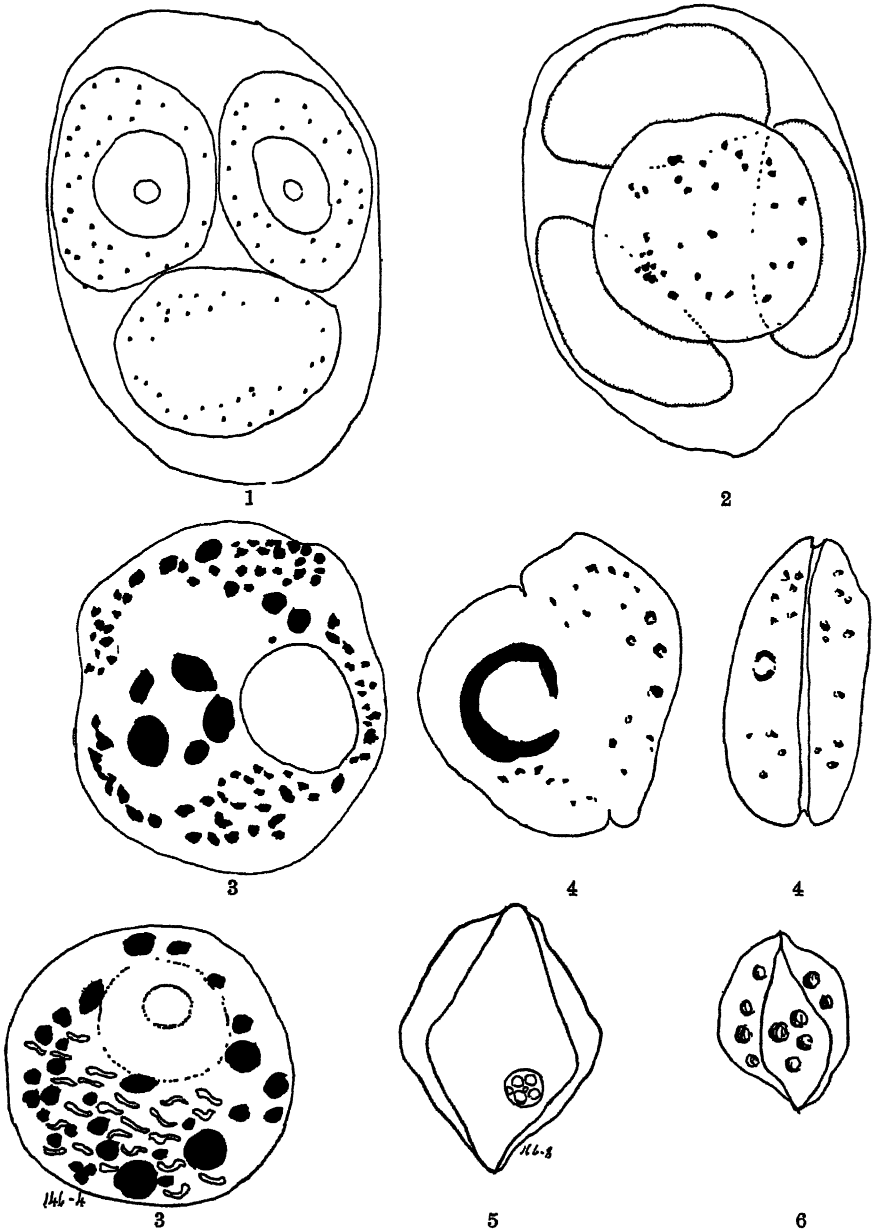

Fig. 1. Evolution of the vacuolar system in normal and abortive pollen grains of monosomic haplo-F *Tabacum* (33146–4). *1, 2,* tetrads containing some large spherical grains where vacuoles (shown black) stain sharply with neutral red as tiny red droplets; no vacuoles can be stained in smaller distorted grains, the whole of which stains a dirty red with neutral red. *3,* pollen grains from unopened flower (33146–4): *upper,* apparently normal, exhibits enlarged vacuoles, the contents of which stain uniformly with neutral red; *lower,* shrunken grains containing small vacuoles, the contents, flocculated by neutral red, outlining the periphery of the vacuole. *4,* pollen grain from opened flower (33146–4) showing the spherical vacuoles (in black), stainable with neutral red. *5,* shrunken pollen grain from haplo-Q *Tabacum* (33166–8) containing a bright inclusion, presumably phytosterol. *6,* shrunken pollen grain showing abundance of fat droplets, which can be stained blue by indophenol blue.

tom in the plant cell. This test distinguishes between viable and unviable microspores rather than between normal and 23-chromosome pollen grains.

Staining pollen grains with nascent indophenol blue demonstrated the presence of tiny oil droplets in the cytoplasm of normal grains. Such oil droplets may be more numerous and larger in degenerating pollen grains, suggesting fatty degeneration; but the most evident bright inclusions in such grains, that is, those which Olmo always found associated with shrunken size, do not stain with indophenol blue. These inclusions may be tentatively supposed to be phytosterol, a material which is likely to accumulate in cells where proper metabolism is inhibited.

CORAL FLOWER COLOR IN N. TABACUM

"Coral" plants were obtained by Clausen, "as a result of a secondary recessive modification of the F chromosome, represented by the symbol F-co." The type is distinctly dwarfed as compared with normal carmine *N. Tabacum.*

"Coral" vs. "carmine" anthocyanols.—Anthocyanols belong to one of two groups: (1) anthocyanols which are red at pH 3 or pH 4, turn to purple about pH 5, to blue at pH 6, to green at pH 8; (2) anthocyanols which are "clear red" at pH 3 to pH 7, and turn to brownish violet tints in alkaline solutions. The anthocyanol of carmine *N. Tabacum* seems to belong to the first group, that of coral to the second. The carmine epidermis turns green when macerated in a solution buffered at pH 8, or when fumed with ammonia. Under the same conditions, coral turns to a purplish brown. The green color of the first anthocyanol, and the brownish of the second, when in alkaline solution, may result from the interference of yellow flavones (Buxton and Darbishire, 1929).

When either the inner or the outer epidermis is stripped off and macerated in a dilute aqueous solution of HCl, carmine yields a cherry red extract, which turns to a bluish green on neutralizing with a saturated solution of sodium carbonate, while "coral" gives an orange-red extract which turns to a dirty violet-blue on neutralization. The distribution number between butyl alcohol and aqueous hydrochloric acid is relatively high, suggesting a monoglucosidal carmine (and coral) pigment. The addition of a saturated picric acid solution to the carmine extract results in separation of needle crystals. The carmine pigment gives a yellowish color with sodium acetate, while coral gives red. The above reactions may be explained by the presence of anthocyanol of the cyanin type in carmine and of the pelargonin type in coral. In discussing a "coral" *Primula sinensis* as contrasted to the pink color of most varieties, De Winton and Haldane ascribe the "coral" pigment to a pelargonidin derivative. Pelargonin derivatives have no phenolic groups in positions available for methylation, and therefore it is not known how pelargonidin can be derived from the common primulin (or malvidin 3-monoglucoside) which is the main pigment of magenta red and blue *P. sinensis*. The "coral" *Primula* appears to be incapable of performing a certain oxidation, and the factor for coral is likened by De Winton and Haldane "to the recessive factor for alcaptonuria in man and to those for white and yellow hair in the rabbits; in each case the recessive form seems to be incapable of carrying out an oxidation."

CYTOLOGY OF CELLS FROM GREEN LEAVES

The mitochondrial technique reveals little fundamental difference in the chondriome of cells in normal, or abnormal *N. Tabacum.* That part of the chondriome which is made up of rod-like, photosynthetically inactive mitochondria, can hardly be expected to be seriously affected by any metabolic change which admits of cell survival. If therefore the plant lives, it indicates that the chromosomal balance is such as to permit the building of normal cytoplasm with normal mitochondria. Changes may be expected, and actually observed, in the proportion of mitochondria which become active photosynthetically. We know that in any given cell, only a certain percentage of them ever differentiate into plastids, some always preserving their rod-like appearance, and remaining, for all that we know, apparently inactive. What percentage change to plastids depends on the metabolism of each cell, and may depend on some factor borne by a given chromosome. That plastids are smaller in haploid and larger in triploid plants than in the diploid was demonstrated by Allen for liverworts and by Wettstein for mosses. That the same relation holds true for tobacco is evident from the comparison of pieces of epidermis stripped off a leaf (or a flower) of an abnormal plant, and at the same hour off a corresponding leaf of an apparently normal neighboring plant. Both specimens could be compared in the living condition, or could be killed *in toto* (in either Regaud's or Meves's solution) to be later stained *in toto,* and mounted in balsam.

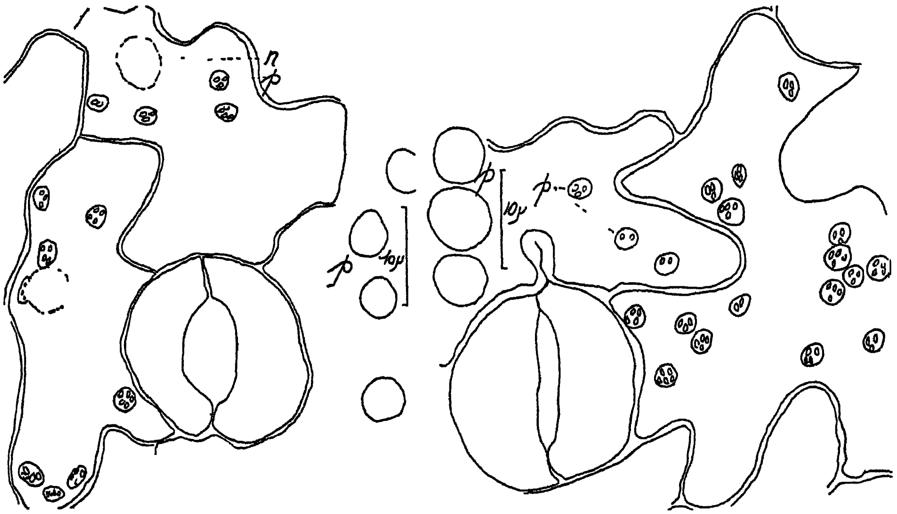

Fig. 2. *Right,* large epidermal cell with large plastids of late-flowering normal F_1 *tomentosa-Tabacum* hybrid as contrasted with (*left*) smaller epidermal cell, smaller plastids, of early-flowering haploid *Tabacum.*

Figure 2 (*left*) shows a small epidermal cell of haploid *N. Tabacum* containing plastids averaging 4μ in diameter. Figure 2 (*right*) shows a larger epidermal cell of an F_1 *tomentosa-Tabacum hybrid,* containing plastids averaging 7μ in diameter. That the difference in size seems to depend primarily on an actual difference in size of mitochondria is made evident by comparison of the chondriome in the following figures: figure 3, haploid—small, thin mitochondria, small plastids; figure 4, haplo-F—short, thin mitochondria, small plastids; figure 5 (*right*), haplo-Q—same condition as in preceding, (*left*), normal: longer and thicker mitochondria, larger plastids; figure 6 (*right*), triploid *N. Tabacum,* monosomic for the R chromosome (3n-2)—cytoplasm densely crowded with large, thick mitochondria and numerous large plastids, in contrast to the short, thin mitochondria of haploid *Tabacum* (*left*).

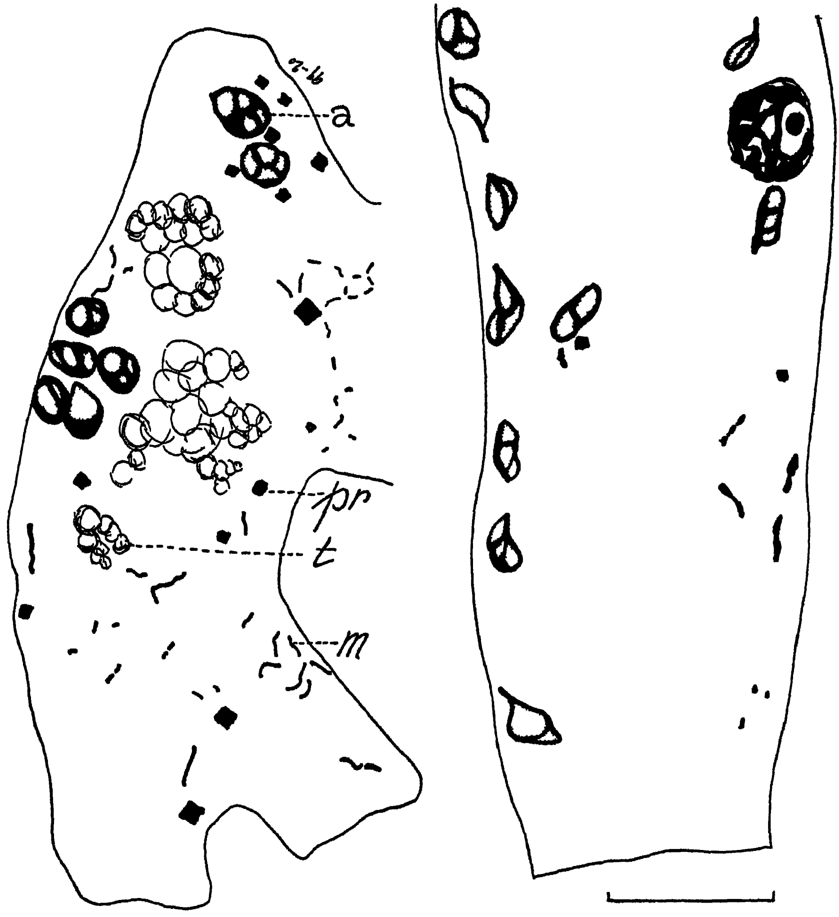

Fig. 3. *Left,* epidermal cell, and, *right,* cell from hair of haploid *Tabacum,* showing small mitochondria (*m*), small plastids crowded with starch grains (*a*), numerous cubic protein crystals (*pr*), and abundant phenolic precipitates within the vacuoles (*t*).

STARCH METABOLISM

The following features have to be considered in starch metabolism:

1. *Differentiation of mitochondria into photosynthetically active chloroplasts of green tissues.*—Actively growing cells, as in bud meristems, have a chondriome made up entirely of rod-shaped, nonsecreting mitochondria. As cells differentiate from the meristematic condition into mesophyll cells of leaf primordia, a certain percentage of these rod-shaped mitochondria differentiate into plastids, which, by developing chlorophyll, become active photosynthetically, that is, develop the ability of building up starch from CO_2.

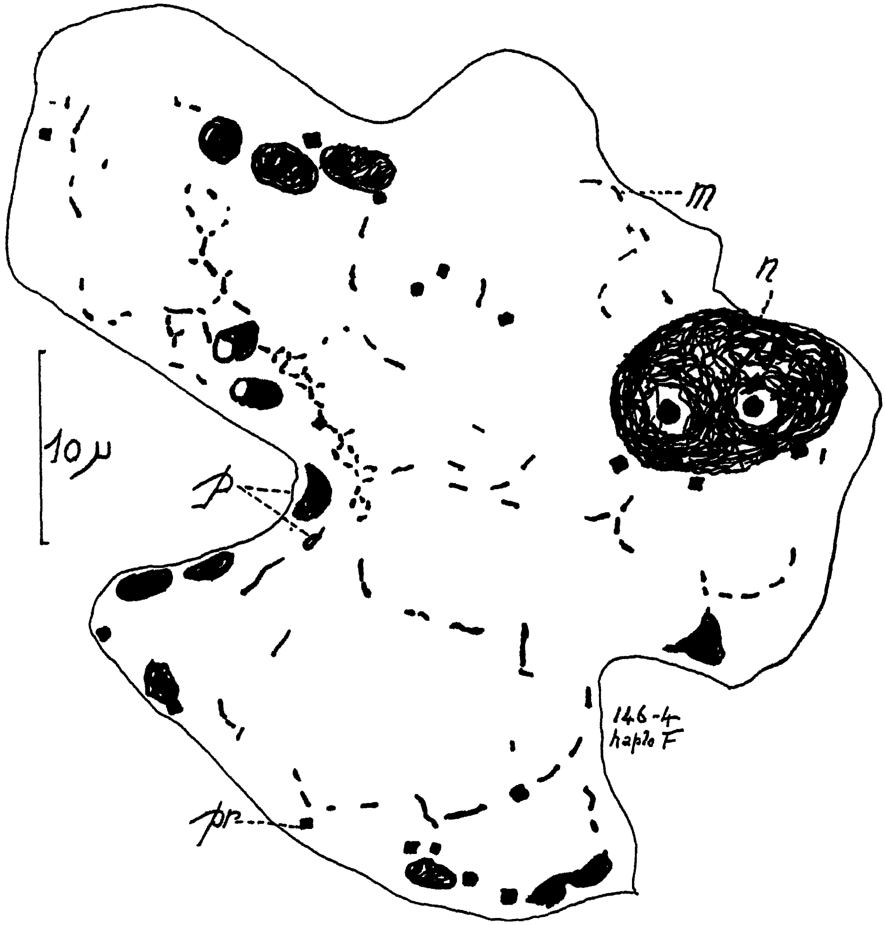

Fig. 4. Epidermal cell of haplo-F *Tabacum* containing small mitochondria, and numerous protein crystals.

2. *Translocation of carbohydrates from the chloroplasts to deeper tissues.*—Inner tissues, mainly meristematic tissues in buds, depend for their carbohydrate nutrition on the translocation of starch, in the water-soluble form of sugar, from the insolated plastids where it is produced. Normally, the chloro-

plasts in the green leaves of tobacco are more or less depleted of starch in the early morning, because of the movement of starch during the night, and they build up a new supply during the day. Translocation of starch from the green plastids to the growing points or storage cells depends on the activity of amylase and is in large measure controlled by the temperature prevailing during the night. It is well known that starch is not translocated from the leaves if the temperature during the night does not keep above a certain minimum. That genetical strains of tobacco differ in their thermic requirements in this respect is indicated by the study of the "coral" types.

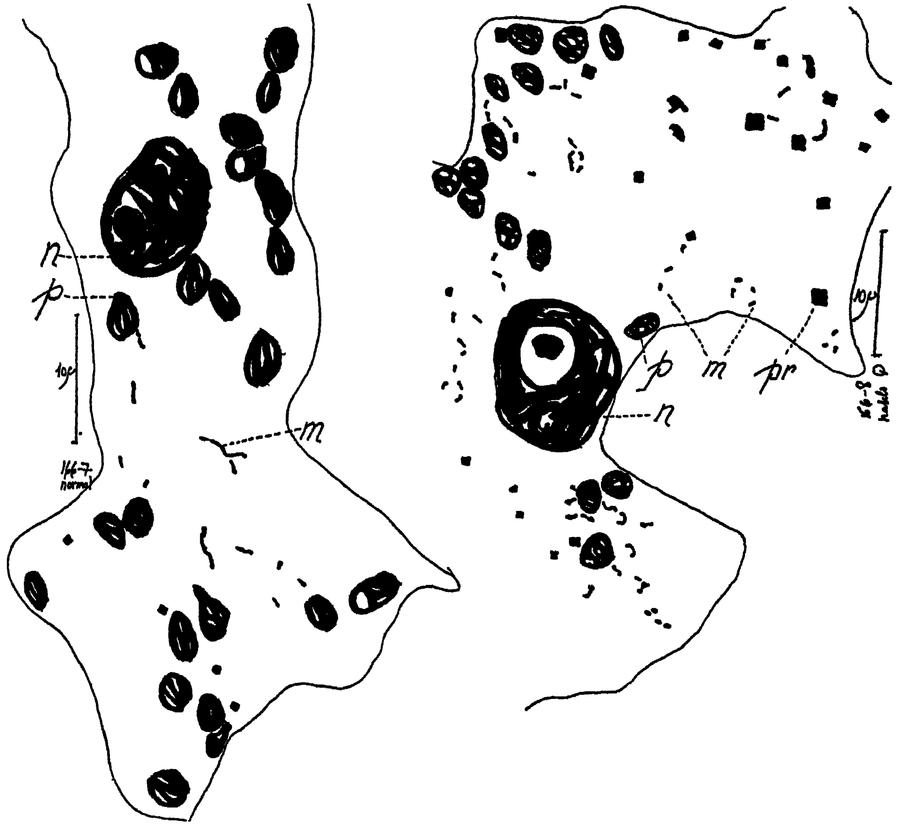

Fig. 5. *Right,* part of epidermal cell of haplo-Q *Tabacum* containing small mitochondria (*m*) and plastids (*p*), numerous large protein crystals (*pr*), as contrasted, *left,* with the normal *Tabacum,* with larger mitochondria and plastids, fewer and smaller protein crystals.

The available carbohydrates are utilized by actively growing cells as a source of energy through oxidation, or as material for the building up of metabolized products; whereas soluble carbohydrates, reaching cells which do not grow actively, are likely to be stored as a surplus in the form of starch grains.

3. *Differentiation of mitochondria into starch-storing "amyloplasts."*—Where more carbohydrates are made available to the cell than can be used up

immediately, the excess is recondensed into starch through the activity of certain mitochondria, which differentiate into amyloplasts. Whereas the production of starch in the chloroplasts is a special function of green plants, the ability of mitochondria to condense sugar is common to both plants and animals. Thus the mitochondria of the liver cells, in storing glycogen, behave in exactly the same fashion as those of plant cells storing starch.

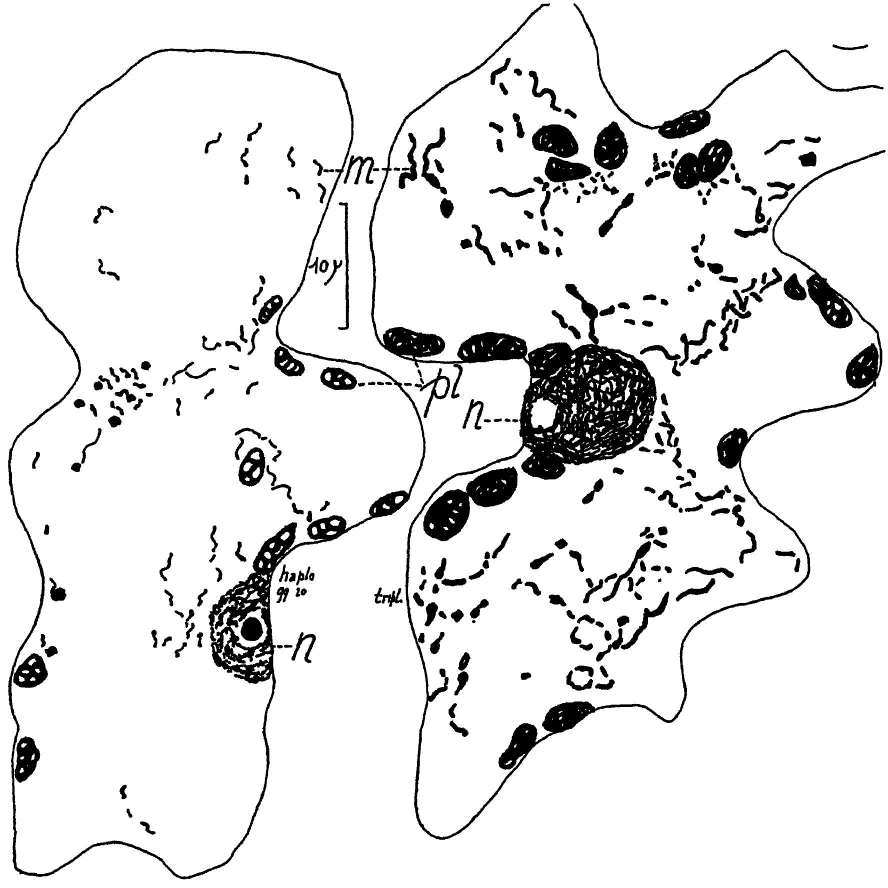

Fig. 6. *Left*, epidermal cell of haploid *Tabacum* (ex haplo-14 *Tabacum* × *tomentosa*) containing small nucleus (about 5μ in diameter), small plastids (3), thin mitochondria, and numerous cubic protein crystals. *Right*, epidermal cell of triploid *Tabacum*, monosomic for the R-chromosome (3n–2), containing a large nucleus (10μ in diameter), numerous large plastids (5μ), and numerous thick and large mitochondria.

4. *Premature storage of starch, concomitant with failure to grow.*—Actively growing cells, such as are normally found in meristems, have a chondriome made up entirely of rod-shaped nonsecreting mitochondria. As one cell loses its ability to grow, some of the mitochondria assume secreting activity, the first evident product of that activity being starch, which is either photosynthesized in insolated chloroplasts or condensed from such sugar as is translocated from green tissues to deeper tissues. Active growth is exclusive of active

starch secretion. Conversely, any inhibition of growth results in premature and excessive starch secretion by the chondriome of the affected cells. This general law is very well illustrated by "coral," and by haploid *N. Tabacum.*

STARCH METABOLISM IN "CORAL"

"Coral" plants are easily recognized by the color modification of the flowers, which was shown by Clausen to be the result of a modification of the F chromosome. "Coral" plants, both of the haplo-F and the normal types, and the nullo-F coral hybrids obtained by crossing haplo-F *Tabacum* with *N. sylvestris,* have smaller, narrower leaves which are tough and brittle when handled. Instead of the normal dark green color, they display a whitish hue. The cause of this peculiar starchy texture and the whitish color is that the chloroplasts remain stuffed with starch grains day and night, through inability to translocate the photosynthesized starch. Figure 7 (haplo-F *Tabacum* × *sylvestris*) shows the huge plastids crowded with starch grains in a cell of the lower epidermis of the "coral" as contrasted with small plastids containing only thin, minute starch grains in a homologous cell of a green leaf of the normal *sylves-*

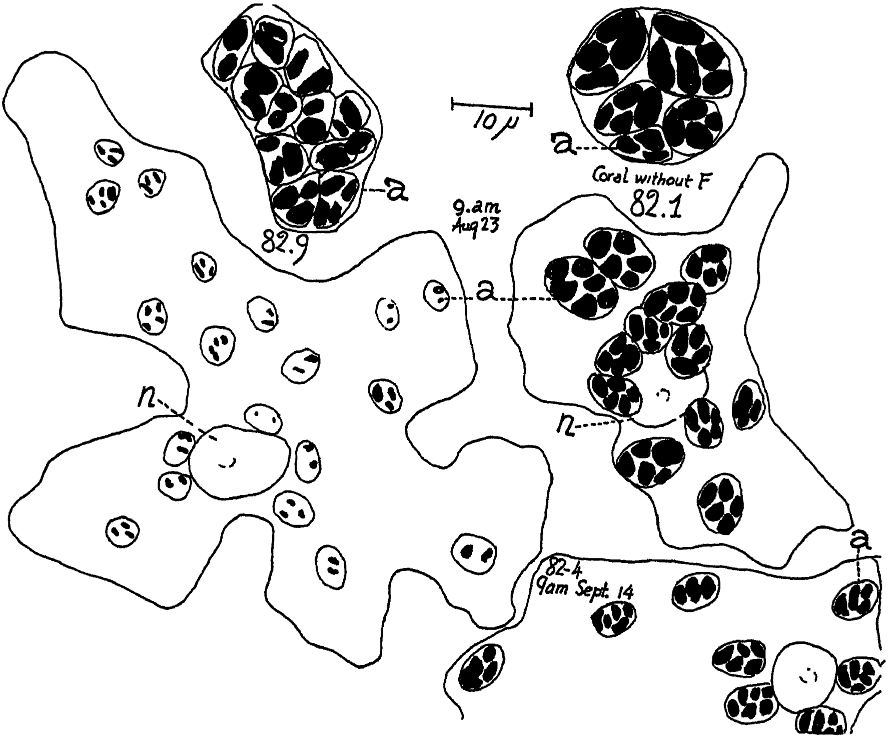

Fig. 7. Mesophyll and epidermal cells of F_1 haplo-F *Tabacum* × *sylvestris*, collected 9 A.M., August 23. *Left,* from normal F_1 *sylvestris-Tabacum,* small starch grains in plastids; *right,* from coral F_1 *sylvestris-Tabacum* (nullo-F type), plastids crowded with starch grains; *lower right,* from coral F_1 *sylvestris-Tabacum* collected 9 A.M., September 14.

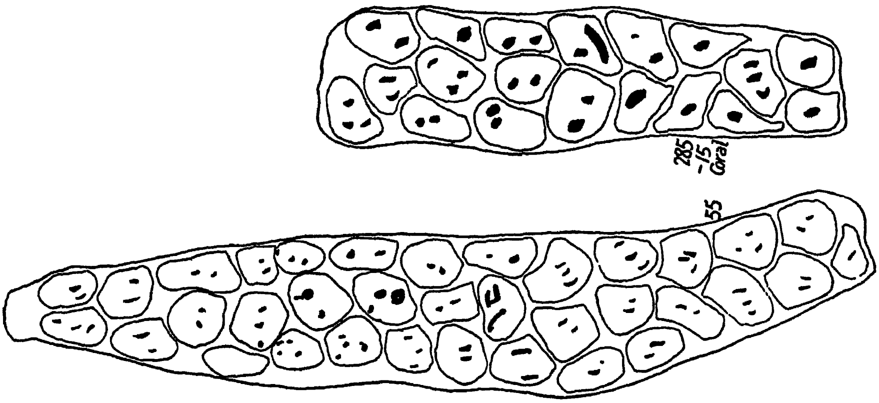

Fig. 8. Palisade cells of normal *Tabacum-purpurea* below, and coral *Tabacum* above, collected at 9 A.M. (starch grains shown black in plastids).

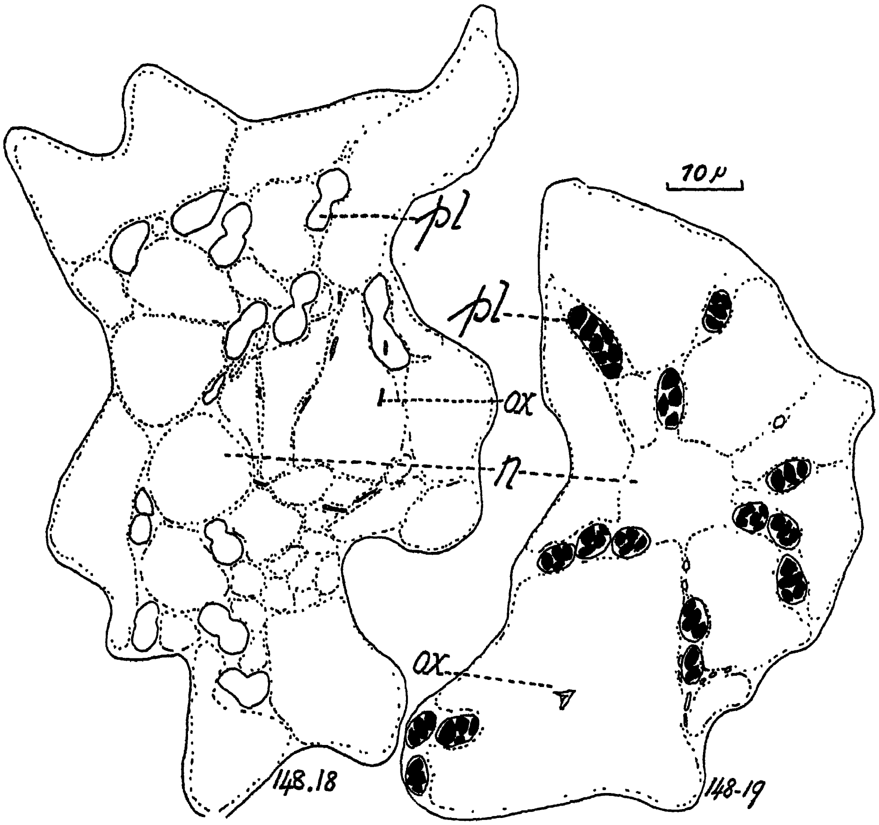

Fig. 9. Cells from lower epidermis peeled at 9 A.M. off leaf 9, from F_1 haplo-F × asynaptic heterozygote; *left*, from normal *Tabacum*, no starch in plastids (*pl*), monoclinic calcium oxalate crystals (*ox*); *right*, from haplo-F coral *Tabacum*, plastids (*pl*) crowded with starch grains, calcium oxalate crystals (*ox*). (The plastids in mesophyll cells were equally crowded with starch.)

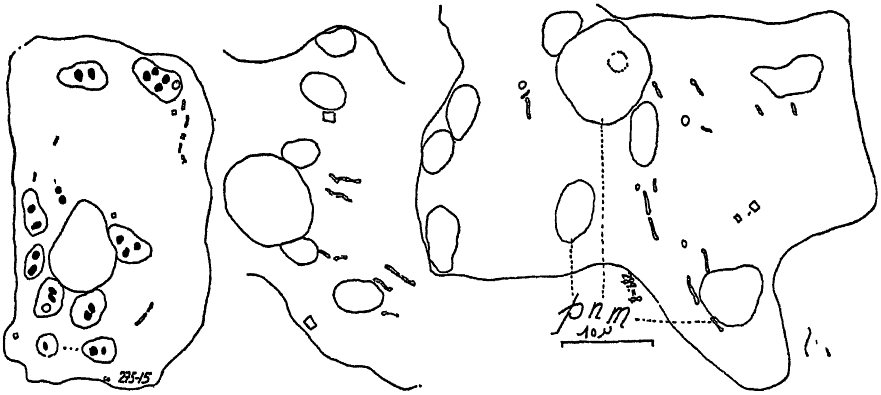

Fig. 10. *Left,* epidermal cells of coral *Tabacum;* middle, normal type carmine *Tabacum;* and *right,* "coral plus" *Tabacum.*

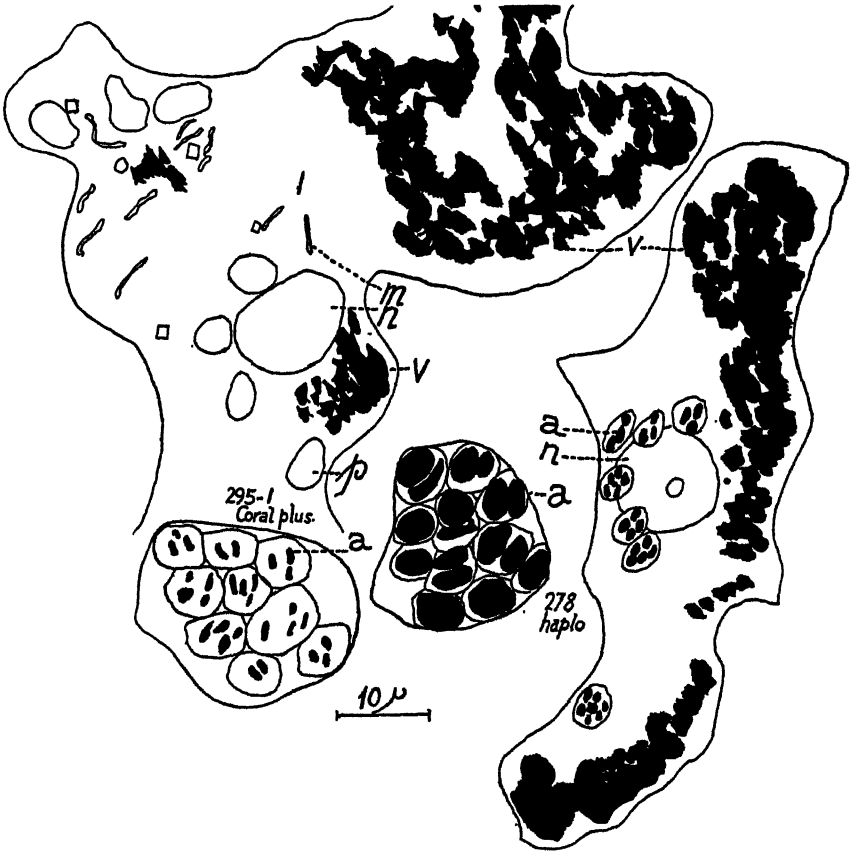

Fig. 11. Epidermal and mesophyll cells collected at 10 A.M. and stained by the I + KI solution. *Left,* from "coral plus" (of the haplo-F "coral plus" × variegated mammoth progeny) showing plastids without starch in epidermis, with minute starch grains in mesophyll cell; long mitochondria (*m*), abundant precipitate of nicotine in vacuoles (*v*). Right, small cell from haplo-F self-carmine showing plasts crowded with starch.

tris-Tabacum hybrid (August 23, 9 A.M.). Figure 8 illustrates the short palisade cell of "coral," as compared with that of normal *N. tabacum.*

Figure 9 shows a lower epidermal cell of a leaf from "coral" with plastids crowded with starch at 9 A.M. on August 7, when those of epidermal cells of

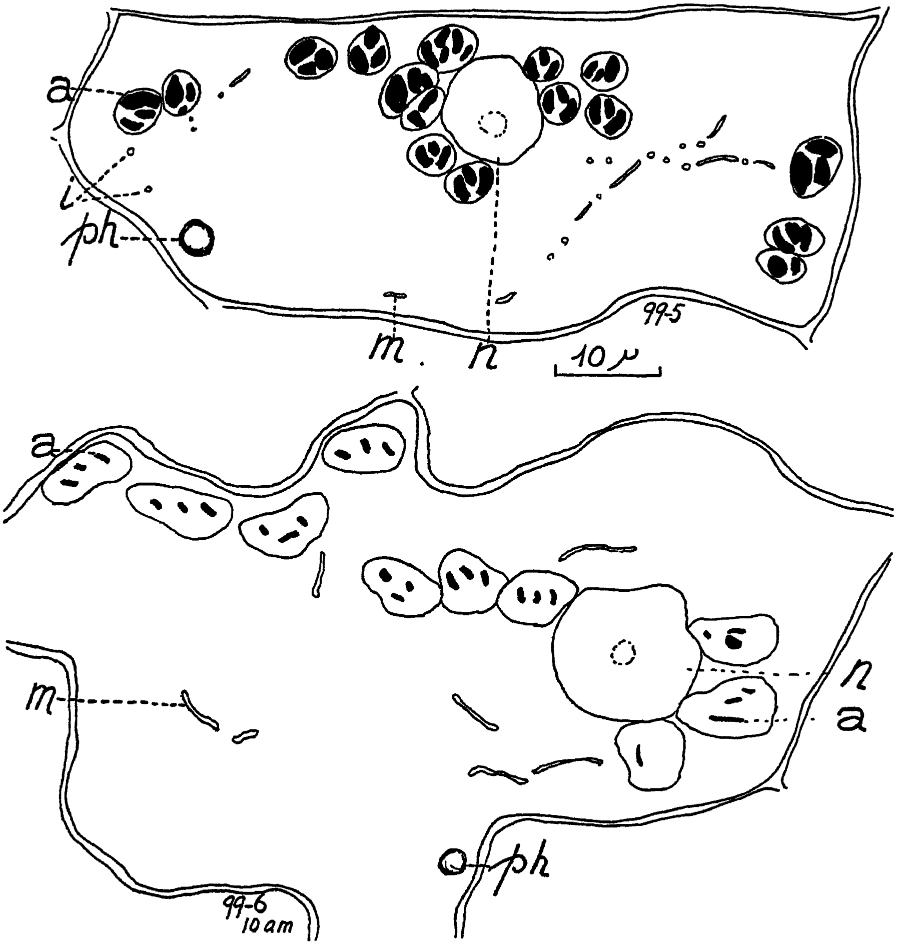

Fig. 12. Epidermal cells from plants of F_1 progeny of the cross haplo-14 *Tabacum* × *tomentosa. Upper,* small cell from haploid, dwarf *Tabacum* with small plastids crowded with starch (*a*) at 10 A.M., small mitochondria (*m*), numerous tiny oil droplets (*i*), and a large spherical refringent inclusion, presumably made of phytosterol (*ph*). *Lower,* large cell from normal F_1 *tomentosa-Tabacum,* showing large plastids containing few small starch grains at 10 A.M., long mitochondria (*m*), and a small spherical inclusion (*ph*).

green leaves of *Tabacum* hybrids of the same progeny, F_1 haplo-F × asynaptic heterozygote, were absolutely devoid of starch. Although the mesophyll cells of "coral" do not show such a clear-cut difference, because the cold nights prevailing at Berkeley do not favor starch translocation even in normal tobacco, still they consistently contain or retain definitely more starch than those of normal *Tabacum.* Although inhibition of starch translocation is a common feature in "coral," it does not seem to be linked with the coral color of flower, but with an inhibition of growth expressed by the dwarfishness of the common "coral." The "coral plus" type, which grows to full size, shows no crowding of plastids with starch grains, but behaves like the carmine type as far as starch translocation is concerned (figs. 10 and 11). Conversely, dwarf haploid plants manifest an inhibition of starch translocation concomitant with the inhibition of growth (figs. 12 and 13).

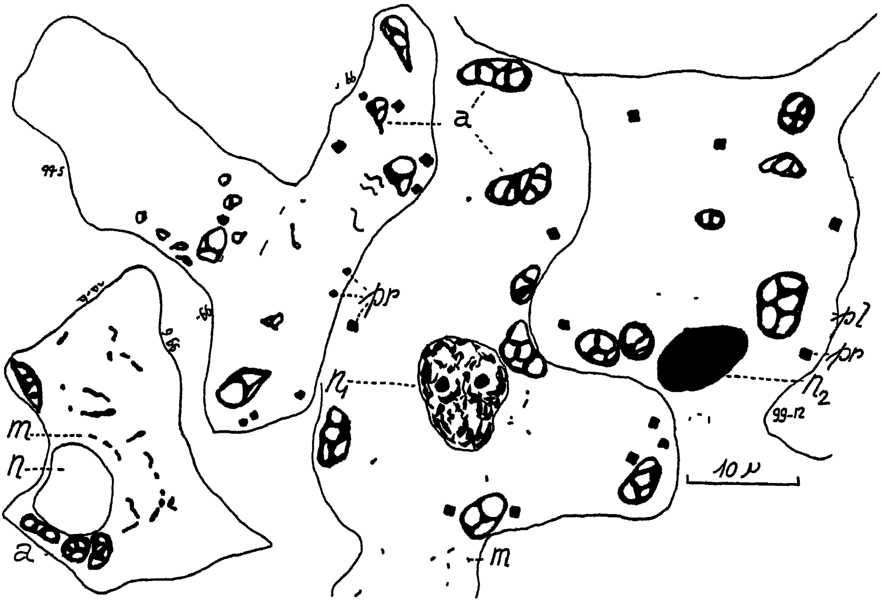

Fig. 13. Epidermal cells from F_1 haplo-14 × *tomentosa* (33099–12) killed with Nemec fluid and stained with acid fuchsin. *Upper left,* small cell from haploid, dwarf *Tabacum,* showing no nucleus and numerous protein crystals, most of the mitochondria differentiating into amyloplasts; plastids retain starch grains during night. *Lower left,* cell from normal *tomentosa-Tabacum* showing numerous inactive, rod-like mitochondria (*m*). *Right,* two cells of 33099–12 showing a fairly normal (n_1) and an abortive nucleus (n_2).

EFFECT OF DARKNESS ON UTILIZATION AND TRANSLOCATION OF STARCH

1. *Starch utilization.*—Green leaves detached from F_1 *tomentosa-Tabacum,* and whitish leaves detached from dwarf haploid *N. Tabacum,* were placed in a dark room on August 7, the cut section of the petiole dipping in water. The green leaves from normal plants used up the starch from the chloroplasts so that no trace was left on August 10, although at the same time the plastids of the haploid leaves were as heavily packed with starch as at the beginning of the experiment. The green leaves cured into soft, light-colored leaves by the end of August, but the starchy ones from the haploid turned to dark, brittle leaves.

2. *Starch translocation.*—The upper branches of a number of *Nicotiana* plants were hooded under black paper, in the field, on August 22. By August 29, lower epidermis stripped off hooded leaves of either "coral" ($12_{II} + 11_I$) or normal ($12_{II} + 12_I$) F_1 *sylvestris-Tabacum* showed no starch, except in the

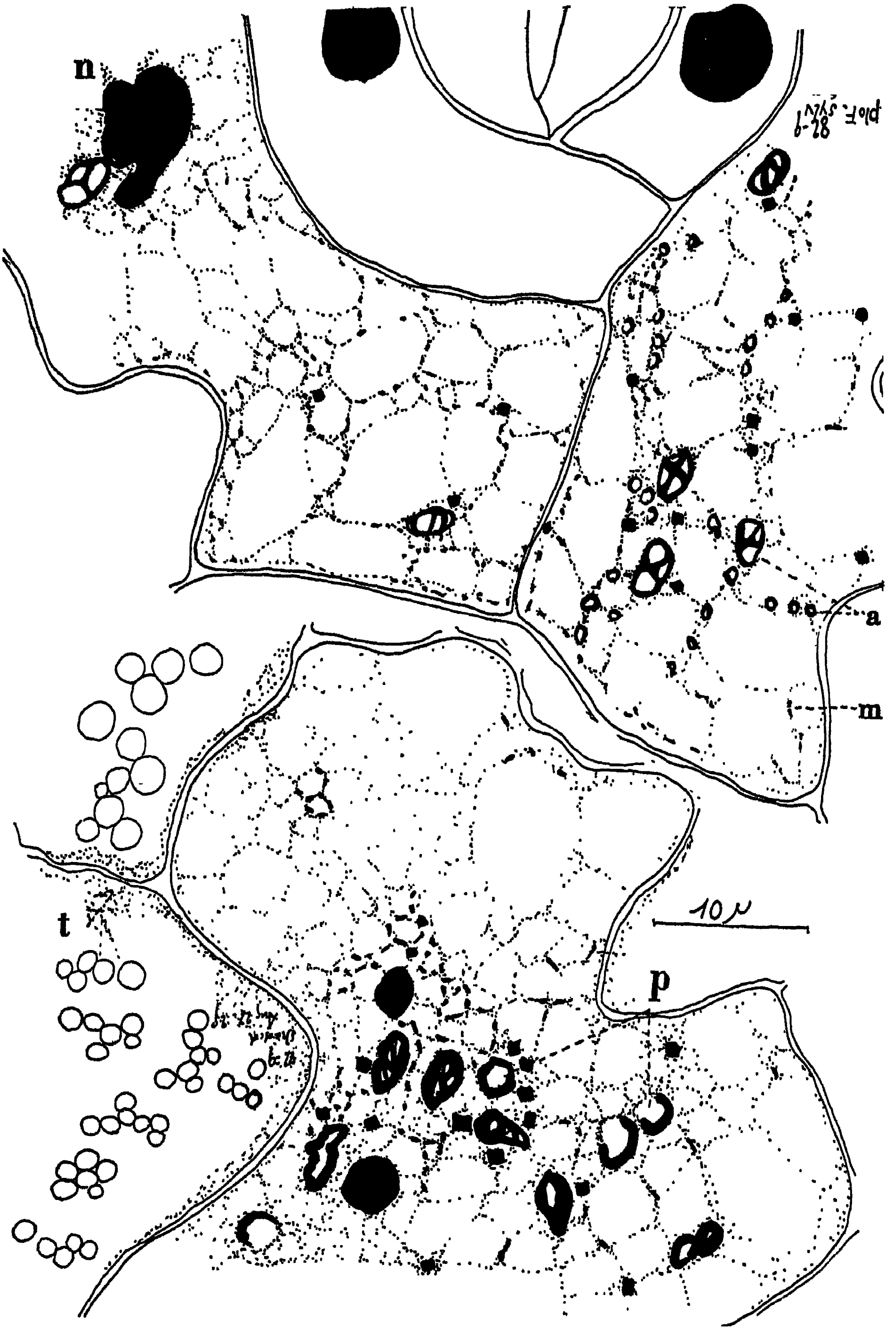

Fig. 14. Epidermal cells of coral F_1 *sylvestris-Tabacum* (ex haplo-F *Tabacum* × *sylvestris*): *upper*, from lower unshaded leaf; *lower*, from upper hooded leaf: *a*, amyloplast; *m*, mitochondria; *p*, plastid; *n*, nucleus; *t*, tannin.

stomatal cells, around ostioles. The plastids in other cells were devoid of starch and much depleted in size; many were elongated, some in the process of division, indicating a tendency to revert to the mitochondrial type. After the hood had been shading the upper leaves of these hybrids for two weeks, the lower epidermis of lower leaves, left exposed to the sun, showed almost all mitochondria secreting starch and differentiating into amyloplasts (fig. 14*a*). Few mitochondria retained their rod-like shape (fig. 14*m*). In sharp contrast, the lower epidermis of shaded leaves showed many rod-like mitochondria, serially lined up along thin films of the honeycombed cytoplasm. Not only had the plastids been depleted of starch, but also their lipo-proteidic substance itself had been drawn upon, only crescent-shaped remnants being left in many. All these cytological symptoms, aggravated by the presence of numerous protein crystals, are precisely those which are constantly observed in the green cell when, as a result of inhibited photosynthesis, it must remobilize the formerly metabolized product, through increased proteolysis. When all available material has thus been used up, the cell enters a period of stress, during which time ante-mortem changes occur, resulting probably in accumulation of amino acids in the vacuolar sap. These, together with phenolic compounds, are easily precipitated by the killing fluids in the form of spherical intravacuolar globules (*t*).

SUMMARY

Many of the heritable characters in *Nicotiana* may be expressed quantitatively through the use of biometrical methods. All those characters, however, which can be measured and expressed as plus or minus deviations from a modal value, are the ultimate, evident expression of differences in cell metabolism. Cell metabolism itself, at least what we can know of it, is the outcome of a set of concomitant processes, many of which are antagonistic. For example, the so-called oxidation-reduction potential is one result of an equilibrium between oxidations and reductions, which may occur at various places within the cell, the vacuoles being generally considered the seat of the more oxidative processes while the cytoplasm seems to be more avid of oxygen and to exact more reducing power. Again, while starch is photosynthesized in the chloroplasts of insolated green leaves, it is also being hydrolyzed into sugar preparatory to translocation. Similarly, while raw nitrogenous materials are being metabolized into amino acids, proteins, and ultimately into the lipo-protein complexes of which cytoplasm, mitochondria, and plastids are composed, some of these metabolized products are remobilized into simpler, or water-soluble nitrogenous materials.

Every aspect of the metabolic activity of the cell has a material basis which, in some occurrences at least, may be recognized under the microscope. We know, for example, that every cell contains mitochondria, and that while a certain proportion of these mitochondria never manifest any evident rôle in cell metabolism, others may and generally do play an evident rôle in synthesizing starch; so that the structural appearance of a cell at any time provides good evidence of its activity in photosynthesizing starch, or in storing up starch through the condensation of translocated sugars. Starch grains are constantly more numerous and larger in epidermal cells of dwarf "coral" or haploid *N. Tabacum* than in actively growing neighboring plants, and it is recorded of some which under examination have shown excessive amounts of starch grains, that, besides the plastids, most of the mitochondria, which normally should remain nonsecreting, secrete and store starch, thereby becoming amyloplasts. Protein crystals are more numerous and relatively larger

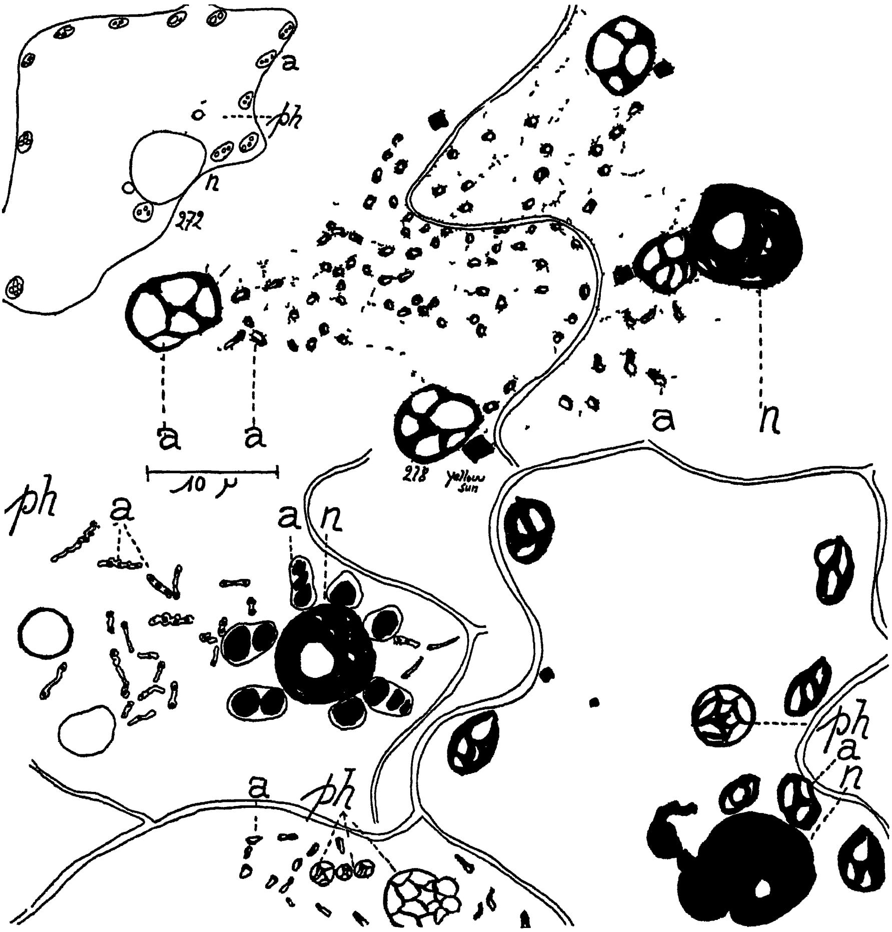

Fig. 15. *Upper left,* epidermal cell of coral *Tabacum,* containing a spherical inclusion, presumably made of phytosterol. *Lower left,* part of lower epidermal cell stripped from a yellowish area on a leaf of haploid *Tabacum* from the F_1 progeny of haplo F self carmine *Tabacum,* stained with I + KI to show mitochondria secreting starch grains (*a*), and plastids crowded with starch grains around the nucleus (*n*); and a bright inclusion (*ph*) presumably made up of phytosterol. *Upper right,* parts of epidermal cells of the same area of leaf, killed with Nemec fluid and stained with acid fuchsin, to show the greater number of mitochondria secreting starch grains and thereby differentiating into amyloplasts (*a*) *Below,* cell showing a phytosterol inclusion (*ph*) above the distorted nucleus (*n*).

in the epidermal cells of haploid or haplo-F *N. Tabacum* than in the normal. Inclusions, presumably made up of phytosterol, are conspicuous in many cells of "coral" (fig. 15) or haploid *N. Tabacum,* probably as a result of inhibited growth. Excessive quantities of phytosterol were detected by Tschen in the tissues of potatoes exhibiting leaf roll, which is investigated in Guilliermond's laboratory, and similar inclusions considered to be phytosterol were observed by Reed and Dufrenoy in "mottle leaf" of citrus. An actively growing cell metabolizes most of the available raw materials into cytoplasm or cytoplasmic inclusions, the constituents of which are so intimately combined as to defy detection through either chemical or physical methods; whereas any growth inhibition will result in the storage of unmetabolized materials in the cell in the form of microscopically visible inclusions, some of which may be identified through microchemical tests.

Genetic differences, as expressed by differences in cell activity, can be represented by the microscopical picture of the nature, distribution, and appearance of the various inclusions in the cell. Therefore these differences, instead of being expressed by tabulating measured characters, have been presented in this paper as camera lucida drawings, each of which tentatively pictures a representative cell of the genotype involved. Each numbered set of drawings presents a pair of contrasted responses, presumably resulting from a pair of contrasted genetic conditions.

A gross relation between the amount of nuclear material and the size or activity of the cell seems to exist, and it might tentatively be assumed that triploid tobacco plants are more efficient in metabolizing living substance than diploid plants; whereas the haploid and, to a less degree, some monosomic individuals are deficient in this respect. These results must be considered to have only a relative significance, chiefly because of the individual differences between adjoining cells in the same tissue. Many of these differences may be ascribed to the unequal repartition of chromosome material, which will be discussed below.

DISTRIBUTION OF ANTHOCYAN IN PINK FLOWERS

Among the Mendelian stocks of *N. Tabacum* grown at the University of California are included three pink-flowering types, which may be conveniently designated as *Tabacum, sylvestris* and *tomentosa* pink. *Tabacum* pink is an old established *Tabacum* type, of unknown origin and widespread occurrence. *Sylvestris* pink is a substitution product derived from the *sylvestris-Tabacum* hybrid. As nearly as may be determined it is phenotypically and genetically the same as *Tabacum* pink. *Tomentosa* pink, a substitution product derived from this *tomentosa-Tabacum* hybrid, is somewhat different phenotypically from the other two types and is genetically distinct from them. All are simple recessives to carmine.

The change from carmine to pink may be the outcome of (1) dilution of anthocyanol in epidermal cells, (2) omission of anthocyanol from either of the two epidermal layers, or (3) occurrence of a mosaic-like blending of full colored, dilute, and uncolored cells in the epidermis.

In *Tabacum* pink and *sylvestris* pink all the cells of the outer epidermis are pink; the inner epidermis is a mosaic of pink and dilute pink cells.

In *tomentosa* pink the outer epidermis lacks anthocyanol entirely, and is made up of uncolored cells; the inner epidermis is a mosaic of full colored (carmine), pink, and dilute pink cells.

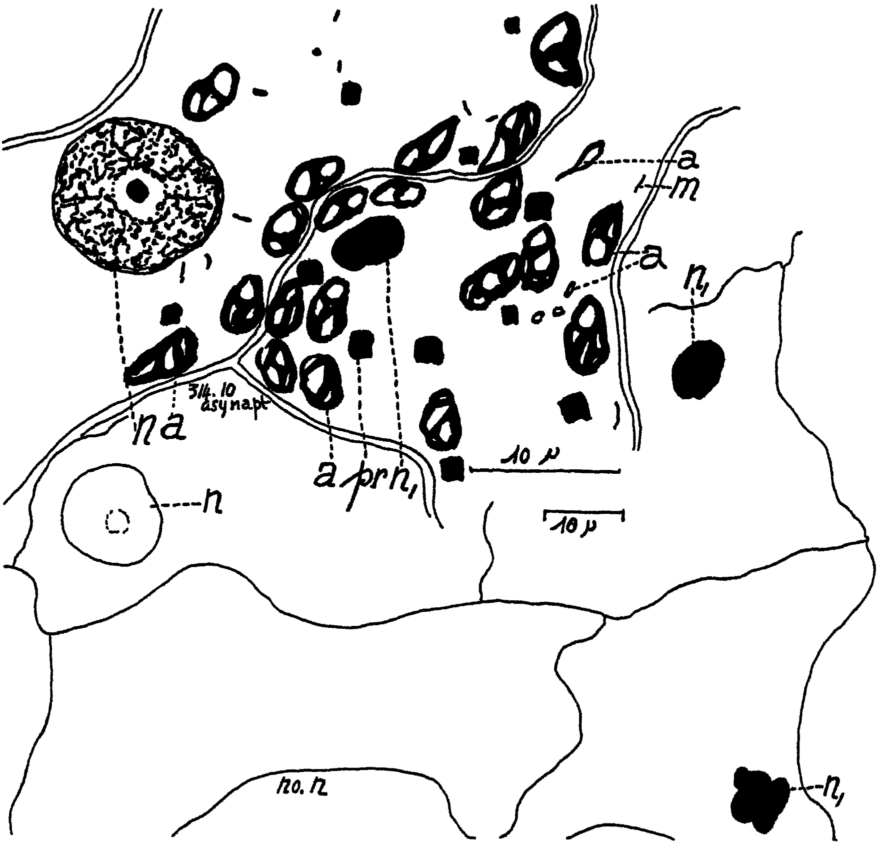

Fig. 16. Epidermal cells of leaf from F_1 hybrid asynaptic *Tabacum* × *tomentosa* pink showing a large nucleus (*n*); or diminutive nuclei (*n'*); plastids containing starch grains (*a*), mitochondria (*m*), protein crystals (*pr*).

IRREGULAR DISTRIBUTION OF NUCLEAR MATERIAL IN SOMATIC TISSUE OF HYBRIDS

Pieces of epidermis stripped from leaves of *Tabacum* haploids (33099–5 and 33099–12) or from certain plants belonging to the highly diverse progeny of asynaptic *Tabacum* × *tomentosa* pink (33314) exhibit areas in which some cells have a full-sized nucleus (fig. 16*n*), apparently normal in structure, with evident nucleolus, while neighboring cells show diminutive, distorted, or misshapen nuclei, which stain more deeply and assume a "lacquered" appearance. In many cells the abortive nucleus is much smaller than the plastids clustered around it, making it all the more inconspicuous. In many other cells, the most careful examination failed to reveal any trace of nuclear material (fig. 16).

GENERAL CONCLUSIONS

VARIED as are the morphological changes exhibited by *Nicotiana,* as the result of hybridization, the effect of various radiations, of viruses, etc., an attempt should be made to link them, first, to alterations in the normal polarity of the tissues, and, second, to inhibitions and correlated exaggerations of certain enzymatic activities in the cells. The relation of inhibition of growth to starch storage in "coral" and haploid *N. Tabacum* affords one way of linking evident phenotypic expression to minute cytological features, and the irregular distribution of nuclear material at mitotic divisions may also be called upon to explain observed distortions and abnormalities; so that eventually it may became possible to explain countless morphological differences as resulting from interactions between slightly unbalanced metabolic processes.

The morphological deviations observed in species of *Nicotiana,* numerous and striking as they may be, depend on alterations of the metabolic activity of the cells in the tissues involved. Any given form of metabolic activity in any cell may be modified only so far as it still permits the other cell activities to proceed, else it is fatal to the cell and leads to necrosis. Any alteration of cell activity involves a corresponding readjustment of cell materials, which can be detected under the microscope; but here again the extent of permissible alterations is limited by the necessity for the different cell constituents to retain certain harmonious relations. So, after all, be its cause a chromosomal disturbance or any foreign stimulus, the range of possible deviations in any form of activity of any given cell is limited to a certain increase (or decrease) of intensity of the corresponding biochemical processes, correlated inversely with a corresponding decrease (or increase) of the antagonistic chemical reactions. Examples of modifications in cell architecture arising from these increased or inhibited reactions, as revealed by microscopic investigations, have been given.

If a logical biochemical explanation of phenotypic differences is to be provided, it should be well understood that:

1. The life of each living cell is the result of an equilibrium among a number of coupled antagonistic reactions.

2. Any reaction is, to a certain degree, independent of the others; although the inhibition of a certain reaction usually favors antagonistic and possibly inhibits correlated reactions.

3. The cytoplasm is not a physiological unit, any more than the nucleus is a genetic unit. Any area of cytoplasm in contact with vacuolar material or with cytoplasmic inclusions has a metabolic activity of its own, which is to a certain degree independent of that in neighboring parts.

4. However, the distribution of energetic processes in the cell and in the tissue results in a certain gradient of energy, which may be made cytologically evident through a polarity of the cell or of the tissues.

Thus all the parts of the plant are correlated so that any change of metabolic activity in photosynthetic cells may bring about very striking morphological alterations in the rest of the plant. We should therefore seek to discover the few general basic laws which govern cell metabolism and the correlation of growth and differentiation, in order to understand more clearly how the addition, omission, or translocation of any chromosome may so profoundly alter the phenotype.

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APPLICATION OF THE ALTMANN FREEZING-DRYING TECHNIQUE TO PLANT CYTOLOGY

II. CHARACTER OF THE FIXATION

BY

T. H. GOODSPEED AND F. M. UBER

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II. CHARACTER OF THE FIXATION*

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T. H. GOODSPEED AND F. M. UBER

IN THE FIRST ARTICLE of this series (Goodspeed and Uber, 1934) reference was made to the necessity of obtaining an adequate nonmineral fixative as pretreatment for microincineration and to the apparent acceptability of the Altmann freezing-drying technique. The character of this type of fixation for plant cells was also briefly noted and some reference was made to the extent to which the technique reveals details of chromosome structure. In what follows comment will be made on the nature of the freezing process in plant tissue and its relation to fixation, particularly of the cytoplasm, after freezing-drying. A third article in this series will deal with new evidence concerning chromosome structure which is revealed as a result of the unique character of the fixation of nuclear constituents by the Altmann technique.

The freezing-drying method involves (*a*) rapid killing by freezing, (*b*) dehydration *in vacuo* of the frozen tissue, and (*c*) imbedding in paraffin. The initial freezing was usually accomplished by immersion of living plant tissues in liquid air. The dehydrating technique, already described elsewhere (Goodspeed and Uber, *loc. cit.*), is applied to the tissue while frozen and, thus, in a condition where diffusion and displacement of cell contents will not occur. Of the two dehydrating temperatures employed, —22° C and —32° C, the latter produced the better results. The vacuum pressure was *ca.* 1 micron of mercury and, with respect to the material referred to in what follows, dehydration was continued for 14 days.

The tissue, after removal from the dehydrating apparatus, was usually placed at once in liquid paraffin and infiltrated under reduced pressure, complete infiltration requiring from one-half hour to two hours. Preinfiltration with heavy paraffin oil (Stanolax), recommended for cytological material by Gersh (1932), increased the infiltration time and did not produce a superior end product. The use of xylol previous to infiltration was beneficial, although nothing was gained by the insertion of absolute alcohol before the xylol treatment. Material dehydrated while frozen tends to become exceedingly fragile. Apparently pretreatment with xylol produces a more delicate infiltration

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* Investigation supported by grant from The Rockefeller Foundation.

which, together with a hardening effect, improves the cytological detail of the final preparation. In general, histological features are well preserved after direct paraffin infiltration, although pretreatment with butyl alcohol may be necessary for thick-walled tissue. Thus, segments of the inflorescence axis of *Kniphofia* sp. subjected directly to hot paraffin and remaining there *in vacuo* for some hours were incompletely infiltrated even after a number of weeks, whereas pretreatment with butyl alcohol decreased the infiltration time markedly and good sections were cut at 10μ.

As was to be expected, the general staining reaction of plant tissues prepared according to the freezing-drying technique was not the same as that of the controls, which were treated with conventional chemical fixatives. Of the few cytological stains employed, Heidenhain's iron haematoxylin proved to be most satisfactory. Even after heavy staining, the time required for differentiation was much reduced as compared with control. In general, the differentiation of chromatin from cytoplasm was not as easy or precise as in control, and mature chromosomes did not present their usual conspicuous appearance as a result of the absence or low chromaticity of their chromonematic matrices. It was noted that starch grains did not stain with haematoxylin, although mitochondria and proplastids were often well differentiated.

In plant tissue frozen at *ca.* —10° C, Molisch (1897) observed either the formation, in intercellular spaces, of ice crystals which grew at the expense of the cell sap, ultimately dehydrating the protoplasm and causing plasmolysis (cf. pl. 1, fig. 1), or a solidification of the contents of the individual cells, which then took on the appearance of a coarse reticulum or network, the interstices being filled with ice crystals (cf. pl. 1, fig. 2). In the latter event, as in the former, the final structural effect was assigned by Molisch to dehydration of all or of portions of the protoplast (cf. Matruchot and Molliard, 1902). Several later investigators, though doubtless aware of the obvious influence of distinctions in morphological and physiological condition of the cells exhibiting different types of reaction to freezing, emphasized almost exclusively the rate of freezing as the determining factor.

In the freezing of human tissues and those of fish, Reuter (1918) found a progressively more reticulate protoplasm the slower the freezing rate. Using carbon dioxide snow on a freezing microtome, he asserted that the structural appearance of the rapidly frozen tissue corresponded in detail to that following fixation by other histological methods known to give favorable results. Reuter refers to this as a preservation of the molecular arrangement, the rapid solidification precluding spatial readjustments. Hürthle (1931), however, who tried both a carbon dioxide snow-ether freezing mixture and liquid air on frog muscle, could not confirm Reuter's results, but found that rapid freezing produced a certain coarsening of protoplasmic structure. With liquid air Hürthle obtained a more reticulate and generally less desirable fixation than with freezing mixtures at *ca.* —70° C. A similar observation is reported by Scott (1933), who points out that freezing under liquid air is retarded by the initial air film which forms between the liquid air and any appreciably warmer object. He suggests the use of ethyl alcohol near its freezing point. In our experience (PMC of *Kniphofia* sp. and *Nicotiana* sp.) nothing was gained by killing in this reagent at —100 °C as contrasted with liquid air killing. It is to be noted that, in either procedure, the tissue will require from several seconds to a minute or more to attain the temperature of the freezing medium surrounding it.

Our results indicate that, given extremely low temperature conditions applied to living material, there are a variety of accessory factors which may determine the character and rate of the freezing process and that for plant tissue the influence of these factors on the nature of the fixation may be predominant. For example, the unknown factor which creates centers of crystallization plays a most significant rôle. In this connection, it is of interest that slow freezing gives rise to such centers at intercellular and nucleocytoplasmic surfaces, or in zones where cytokinesis is occurring. Where freezing is rapid, the number of centers is important in the determining of the degree of reticulation produced.

It is to be noted, also, that cell walls and protoplasmic membranes may act as very effective heat insulators and prevent the transmission of crystallization stimuli across the boundaries they form. Thus, in the micromanipulation studies of Chambers and Hale (1932), it was shown that, in slow freezing, when crystallization began in an intercellular space it was in large measure restricted to that area, with consequent dehydration of neighboring protoplasts, rather than extended across protoplasmic membranes so as to cause uniform freezing. Similarly, the degree of supercooling is influenced by such barriers, and in general it is clear that the rate of cooling of intact living tissue is not an arbitrary condition to be imposed solely from without, but that it may be affected by the structural and physiological differentiations peculiar to the tissue under investigation.

We have been concerned with the character of the fixation by the freezing-drying technique of Altmann in meristems of root tips and in somatic and reproductive tissues of immature anthers of *Lilium longiflorum* at different stages of development. If a relatively homogeneous structure of cytoplasm and nucleoplasm in microscopical preparations of such tissue is taken to be a reflection of "good" fixation, the results of freezing-drying are by no means uniformly "good" for the material referred to. Varying degrees of coarseness or reticulation, which at times may assume a directional or striated form, are characteristic of the structure of the resting or prophase nucleus and of the cytoplasm. The fact that longitudinal striations in nucleus and cytoplasm may often extend uninterruptedly across groups of cells strongly suggests extreme supercooling followed by rapid crystallization. Such a phenomenon cannot be externally controlled.

The correlation of the character of fixation with the position of the cells in a tissue undergoing freezing indicates with unusual clearness the nature of the process involved. Thus, in young anthers of *Lilium longiflorum,* for example, the PMC near the surface of the anther sac exhibit a type of fixation different from that of PMC more distant from the surface. The line of demarcation between the two is usually sharp, and adjacent cells and even halves of the same cell may show a quite different quality of fixation. The photomicrograph shown in plate 1, figure 1, illustrates this point. The coarse reticulation to be seen toward the exterior of the section is undoubtedly caused by rapid crystallization, and farther inward the finer structure is a product of cell dehydration to intercellular cavities. That the line of demarcation between nucleus and cytoplasm is often seen to be a center of crystallization tends to lend support to Scarth's (1927) contention that the nuclear membrane may be double. Bensley and Gersh (1933) found a similar condition to obtain in animal tissue after freezing-drying and were able to obviate the unfavorable fixation of peripheral cells by enclosing the piece of tissue under investigation within a second tissue layer before freezing. This result is to be interpreted, in our opinion, as the product of a partial dehydration of the inner block of tissue preceding its actual freezing. The surrounding tissue layer freezes first and withdraws superfluous water from the inner tissue mass, with the result that the protoplasm of the latter subsequently freezes without the formation of ice crystals. It should also be noted that Bensley and Gersh (*loc. cit.*) withheld water from experimental animals for a twenty-four-hour period preceding fixation. Unfortunately, the degree of hydration in plant material is not so readily susceptible to external control. It therefore appears that the quality of the cytological fixation of plant tissues cannot be as precise as that of animal tissue, the presence of cellulose walls, an elaborate intercellular space system, and the apparent necessity of maintaining a high degree of hydration in living plant cells accounting, at least for the most part, for this distinction. Nevertheless, specific reactions to freezing-drying on the part of plant cells and their constituents give this technique a peculiar significance.

The reaction of various types of cells and of cells at different stages of the mitotic and meiotic cycle to freezing are likewise significant. Thus, the tapetum, although showing a certain coarseness in protoplasmic structure, was uniformly more resistant than neighboring tissues to what is taken to be alteration of the living structural condition. The resting nuclei of late archesporial tissue, as well as of meristems of root tips, are rather well fixed, in contrast to the poor fixation of early- and mid-mitotic and -meiotic prophase stages (pl. 1, figs. 1–5). In the latter, fixation progressively improves as metaphase approaches, and remains good in pollen mother cells until the end of the second division. Thereafter the tetrads of microspores and early stages in pollen grain formation show, again, poor fixation. In this sequence there is evidence of distinction in physiological state and particularly in degree of hydration of the tissue involved. From other evidence hydration appears to be increased, during early meiotic prophases at least.

The technique is useful for the study of the achromatic figure and cytokinesis in plant cells. Spindle fibers are as clearly shown in stained preparations after freezing-drying (pl. 1, figs. 3 and 4) as they are after any other technique, a fact which, perhaps, gives further evidence concerning identity of the achromatic figure in the living cell. Certainly this result suggests variations in viscosity or degree of hydration in the cell area occupied by this figure. At late telophase a system of fibers in the equatorial zone was evident, but no appreciable swellings in the mid-zone of these fibers were apparent. However, a definite film or plate was present in the equatorial region, suggesting a localized increase in protoplasmic viscosity. Later a whitish band appeared there and gave the impression that cytokinesis was under way. Comparisons with control indicated that this was a premature cleavage, probably the result of crystallization in a cell plate which, when first formed, is of a fluid consistency (cf. Sharp, 1934, p. 161, 171 *et seq.*).

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DESCRIPTION OF PLATE

PLATE 1

Photomicrographs showing character of the fixation by the Altmann freezing-drying technique in anthers of *Lilium longiflorum* (figs. 1–4) and in root tip of *Narcissus* sp. (fig. 5), 7μ, stained with Heidenhain's iron haematoxylin, Leitz "Makam."

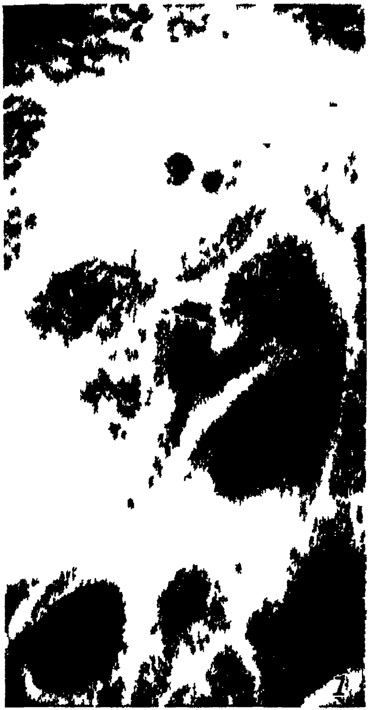
Fig. 1. Archesporial tissue; coarse reticulation at upper left caused by rapid freezing, clear inter- and intracellular areas formed by ice crystals; × 675.

Fig. 2. Heterotypic midprophase; coarse reticulation in nucleo- and cytoplasm; × 810.

Fig. 3. Heterotypic metaphase; fine structure of cytoplasm preserved, chromonematic chromosome structure shown, achromatic figure conspicuous; × 810.

Fig. 4. Heterotypic anaphase; fixation as in figure 3, details of chromonematic structure shown; × 1425.

Fig. 5. Good preservation of resting and late telophase nuclei, clear intercellular areas as in figure 1; × 810.



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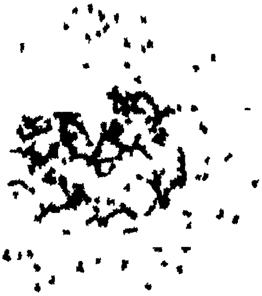

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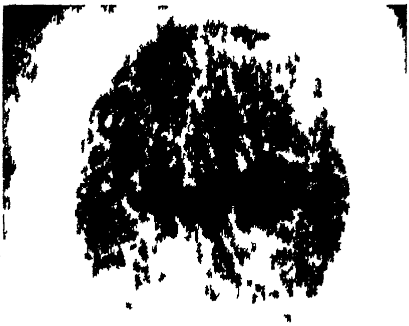

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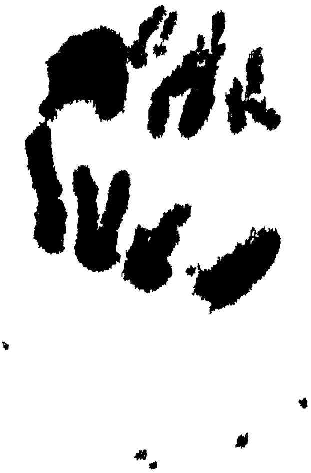

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APPLICATION OF THE ALTMANN FREEZING-DRYING TECHNIQUE TO PLANT CYTOLOGY

III. CHROMOSOME STRUCTURE IN LILIUM LONGIFLORUM

BY

T. H. GOODSPEED, F. M. UBER, AND P. AVERY

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III. CHROMOSOME STRUCTURE IN LILIUM LONGIFLORUM[1]

BY

T. H. GOODSPEED, F. M. UBER, AND P. AVERY

BECAUSE OF their significance for genetic theory, no cytological problems are receiving more detailed study today than those concerned with chromosome structure. The recent evidence obtained by Nebel (1932*a, b,* 1933), Painter (1934*a, b*), and Kaufmann (1926*a, b,* 1931*a, b*), for example, bears directly upon certain theories concerning the relation of mitosis to meiosis. Our special interest in these fundamental problems is derived from their relation to a variety of investigations in cytogenetics and experimental cytology now being carried on in the University of California Botanical Garden. The present communication reports results obtained as a by-product of an investigation of the nature and disposition of fixed minerals in the plant cell as shown by microincineration. As elsewhere noted (Goodspeed and Uber, 1934), the freezing-drying technique of Altmann is valuable in revealing the internal structure of the chromosome. Although this technique does not, as previously shown (Goodspeed and Uber, 1935), produce uniform fixation in all plant tissues, it does often exhibit chromonematic details with remarkable clearness, and, in particular, demonstrates details of internal structure at those stages in the chromosome cycle which in the past have been found difficult to analyze.

This unique by-product of the freezing-drying technique results from a tendency to obliterate or render nonstainable the chromosome matrix (the "rinde" of Ellenhorn, 1934) which, following conventional fixation, is deeply stained and, thus, in large measure obscures evidence of the internal structure of the chromosome. Differences between the extent or rate of freezing of the matrical material and of the chromonemata presumably account for the almost complete nakedness of the latter after Altmann treatment. Thus, at the temperatures employed, the more fluid matrices may become frozen while the less fluid chromonematic material will remain unfrozen, or the latter, being more viscous, may freeze at a slower rate than the former and therefore undergo a more severe dehydration. At any rate, both freezing and drying undoubtedly contribute to the clearness with which structural details in the chro-

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[1] Investigation supported by grant from The Rockefeller Foundation.

mosome are seen, a point which recalls the fact that in the studies of chromosome structure by others the dehydration of the chromonemata (Sharp, 1929; Nebel, 1932) or the alteration of the matrices (Kuwada and Nakamura, 1933; Sakamura, 1927) have been successfully employed. The accompanying photomicrographs (pl. 2) indicate the character of the evidence upon which the following comments are based.

The internal structure of the chromosome, during that portion of the mitotic sequence identified as late prophase to mid-metaphase, has heretofore been found difficult to analyze because of the heavy staining of the matrices after conventional techniques. In our frozen and dried material these stages exhibit the chromonematic constituents and their arrangement with particular clearness (cf. pl. 2, figs. 9 to 15). But to interpret and evaluate this evidence properly, it is first necessary to examine the structure of the anaphase chromosome in Altmann preparations.

At anaphase a network of chromonemata occurs, the line of cleavage between the potential chromatids often not being distinctly developed. Superposition of elements of the network may make it difficult to determine strand number and arrangement, which, however, can be analyzed in cut sections of chromosomes. Our evidence shows that the anaphase chromosome contains four chromonemata—two, possibly intertwined, in each potential chromatid, the two sets of bipartite chromonemata lying parallel. On occasion, freezing-drying tends to separate the two bipartite chromonemata and at the same time may cause coalescence in twos to give an impression of a two- rather than a four-strand internal structure for the entire anaphase chromosome. Ordinarily, however, it is not difficult to follow the course of at least three separate chromonemata at anaphase.

The anaphase chromonemata are delicate filaments which, in our material, increase in distinctness during telophase and the transformations producing the resting or metabolic stage. On the assumption that after freezing-drying the matrix is invisible, the chromatin of the anaphase chromonemata produces the anastomosing threads which give the reticulate appearance to the resting nucleus. The arrangement of "tassement polaire" chromosomes in the form of a hollow cone is well shown in some of our preparations, as is the folding over of the ends of the cylinder to produce initially a hollow, spherical resting nucleus in which the chromonematic network and its anastomoses is in large part peripherally disposed.

The transformation of the much coiled and possibly interwoven anaphasic chromonemata into the delicate, regular peripheral network of the resting nucleus can be followed with some success in our material. Thus, in telophase, the coiled threads become elongated and straightened, and, if previously intertwined, become free from one another, so that at late telophase four independent parallel strands are present in each chromosome tract as described by Nebel (1933) for *Tradescantia*. These four parallel threads remain equidistant one from another in the form of a square throughout the resting stage so that its peripheral network consists of two similar layers, one below the other. Where, in our material, the fixation is particularly "good," the network is too delicate to be accurately analyzed, but where a coarser fixation occurs, involving a certain coalescence of the elements of the network, the condition described above is to be clearly seen (pl. 2, fig. 6). In general the reticulum appears to consist of minute chromatin granules connected by weakly staining filaments.

Bensley (1933) has seen in resting nuclei of frozen-dried mammalian somatic tissue "a chemical structure due primarily to the segregation of the chromatin in special locations." In addition, he says, "the various chromatin particles seem to be connected into a net work . . . by strands of a substance which have a certain degree of chromaticity." As already indicated, a similar, generalized statement may be made for our material, and, in addition, the network we have observed (pl. 2, fig. 6) is more susceptible of cytological analysis than is that shown in the photomicrographs submitted by Bensley.

The first evidence of the onset of prophase is seen in the approximation of certain strands of the reticulum so that chromosome tracts become distinctly visible, the network in each tract consisting of at least four filaments (pl. 2, fig. 7). This and the resting stage deserve additional study in frozen-dried preparations. At late prophase, however, striking evidence of a characteristic internal differentiation of the chromosome is provided. The four-strand early prophase network becomes a series of rather heavily staining "ladders," the chromonematic "sides" of each "ladder" being distinctly thicker than the early prophase filaments and often decidedly chromomeric, and the runglike, slender anastomoses connect the chromatids on the two sides of the ladder (pl. 2, fig. 11). Apparently it is characteristic of a certain period in the late prophase progression that the four-strand continuity with the early prophase structure is temporarily obscured as a result of the close approximation of strands two by two, that is, two strands form one side of the ladder and two the other side. As late prophase passes into early metaphase the characteristic four-strand structure becomes again apparent, particularly at the ends of chromosomes (pl. 2, fig. 8) or where anastomoses pull apart the two strands which form each side of the ladder (pl. 2, figs. 9 and 13). The configuration of late prophase and early metaphase chromosomes, in our material, suggests the onset of a coiling of the strands which were uncoiled at the previous telophase to give the resting reticulum with four independent strands in each chromosome tract. Thereafter the lengthwise contraction and condensation of early to mid-metaphase chromosomes involves disappearance of the ladder with its "rung" anastomoses and production of four independently coiled chromonemata, all lying parallel, the two chromonemata in each chromatid being closely approximated (pl. 2, figs. 14 and 15).

At mid-metaphase, chromosome ends often show the 4-partite chromonematic structure very distinctly. In addition, where these ends could be brought to sharpest focus, the double nature of at least some of the four chromonemata was clear. Our evidence here is sufficiently definite to constitute proof that the mid-metaphase somatic chromosome of *Lilium longiflorum* is 8-partite; in other words, that, by metaphase, each of the four visible chromonemata is double. Such an internal structure at metaphase indicates that the initiation of the division to be accomplished at the anaphase occurred three mitotic cycles earlier. One must postulate that chromosome division, and, more specifically, chromonema division, is a product of initial gene division which is then followed by interaction between the daughter genes and their immediate protoplasmic environment to produce the visible daughter chromonemata. If gene division is thought of as occurring at the culmination of the resting or metabolic stage, the period covering the prophases and early metaphase is none too long to permit the elaboration of a visible chromonema. In accordance with the foregoing, the portion of the mitotic sequence from earliest prophase until cleavage involves 8-partite chromosomes made up of four visible chromonemata, each containing two daughter gene-strings undergoing growth and differentiation, while anaphase, telophase, and a portion of the resting stage involve 4-partite chromosomes.

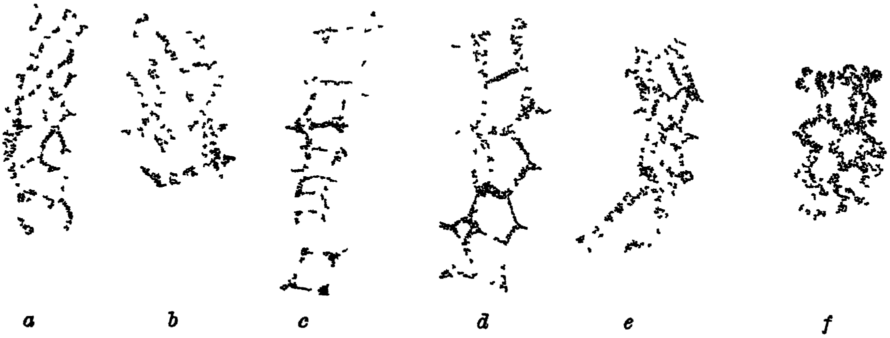

Fig. 1. Mitosis in *Lilium longiflorum* (composites from camera lucida drawings), × 5500. *a*. Anaphase, four chromonemata, two in each chromatid, which may be intertwined or independently coiled and closely approximated; *b*. late telophase, end of a chromosome, straightening and elongation of the four chromonemata, in some regions the two chromonemata of a chromatid have coalesced; *c*. "resting" stage, portion of a chromosome tract, two of the four chromonemata visible, near left center altered orientation shows three of the four, cross-section below; *d*. early prophase, conjugation of parallel threads to produce typical ladder-like stage in somewhat later prophase; *e*. late prophase, separation of the two chromonemata of each chromatid which have been closely conjugated during ladder-like stage; *f*. metaphase, four independently coiled and closely approximated chromonemata, their ends seen to be composed of two daughter chromonemata, giving an 8-partite structure to the metaphase chromosome.

In text figure 1 is portrayed the chromonematic sequence which we have observed in mitoses in anther walls of *Lilium longiflorum*. These drawings are reproductions of camera-lucida studies of short chromosome segments in which structural details were particularly distinct, and are semidiagrammatic only in the sense that, sometimes, combinations of several such drawings illustrate a particular stage. The mitotic sequence shown in text figure 1 may be summarized as follows: (1) the anaphase chromosome contains four visible chromonemata; (2) during the resting stage the four chromonemata maintain their identity as a group of four independent parallel strands lying equidistant from one another in both planes, but connected by anastomoses; (3) sister chromonemata may "conjugate" in prophase, with a consequent obscuring of their 4-partite character, which once more becomes evident in late prophases; and (4) at metaphase an 8-partite chromonematic complex becomes visible, and at anaphase each of the four chromonemata of the daughter chromosome first becomes entirely independent.

There are a number of special problems which require further study in our material. Thus, it is not certain whether the tight coiling of the four anaphase chromonemata is a product of intertwining of two sister chromonemata, or whether all four are independent from the time of their origin when the genes divide in the resting stage and, therefore, that the apparent intertwining represents only close approximation of independently coiled chromonemata. The evidence which we have at hand favors the first alternative, whereas Nebel (1933) describes the second as characteristic of the telophase chromosome. Again, the question of the origin and nature of the anastomoses, although studied from different points of view by various investigators, has not been satisfactorily answered. In maize, McClintock (1934) believes that "the matrix substance of the chromosomes sends out processes which anastomose with one another," whereas Kaufmann (1926*a*) holds that anastomoses are active outgrowths of the chromonemata themselves. In our material they appear to be continuous with the chromatin of the chromonemata.

The structural peculiarities of salivary gland chromosomes of *Drosophila* are interpreted by Bridges (1935) on the basis of a "cable of 8 + 8 strands." The evidence submitted above that, at metaphase, somatic chromosomes of *Lilium longiflorum* are 8-stranded, is pertinent in this connection. According to the scheme of the mitotic sequence outlined above (text fig. 1), the structure of the salivary gland chromosome may be interpreted as follows: (*a*) onset of normal gene division, which is taken to occur at the close of the resting stage, and, thus, formation of eight "gene strings" which represent the primordia of eight chromonemata; (*b*) a suspension of chromonemata building and of the formation of matrical substances after the production of a gene-string on which "gene-chromatin" has accumulated about the individual genes; (*c*) the banded appearance of the 8-stranded chromosome is referable to such accumulation of gene-chromatin, as is evidenced by the relation between visible bands and known genes (Painter, 1934*b*); (d) the chromosomes become greatly enlarged and thus permit determination of cytological details not ordinarily demonstrable; (*e*) association in pairs of the 8-stranded chromosomes.

Evidence relating to the internal structure of the chromosome as supplied by meiotic stages in PMC prepared according to the freezing-drying technique is in accord with that which has been summarized above with respect to mitosis. Concerning the meiotic sequence the following points have been established and provide corroboration of the conclusions derived from the mitotic evidence. Thus, in the portion of a diakinesis shown in plate 2, figure 1, three of the four chromonemata are visible in each member of the bivalent. The polar view of IM shows twelve bivalents (pl. 2, fig. 4), within all of which chromonemata can be seen, although their number cannot readily be determined in every bivalent. Differences in orientation of the different bivalents in plate 2, figure 4, permit different interpretations of their structure. Thus, certain chromosomes appear to be composed of one, others of two, whereas careful analysis of structural details in those which are properly oriented indicates the presence of at least four chromonemata. The side views of a bivalent in plate 2, figures 2 and 3, give better evidence of structural conditions. In these photomicrographs the division of each bivalent partner into two well-separated chromatids is apparent (pl. 2, fig. 3), and the end of each of the four chromatids reveals its double character, as shown at the ends of the short arms of the bivalent in plate 2, figure 2.

A 4-partite anaphase chromosome is, as indicated above, characteristic of mitosis. Chromonematic structure at IA is shown in plate 2, figure 5. A darker printing (Goodspeed and Uber, 1935, pl. 1, fig. 4) of the photomicrograph shown in figure 5 gives evidence concerning the relation of the chromosomes to the achromatic figure and of the latter to the cytoplasm and, further, shows something of the fixation of the cytoplasm according to the Altmann technique (Goodspeed and Uber, *loc. cit.*). The lighter printing, shown in plate 2, figure 5, better reveals the network formed by the four chromonemata, which can be fairly well analyzed, even at the single focus shown in the photomicrograph. It is certainly clear that three strands occur at the mid-point along the left-hand chromatid of the second chromosome of the lower chromosome group. Thus, the chromonematic structure of the meiotic chromosome corresponds to that to be expected according to the mitotic structural sequence outlined above and illustrated in text figure 1.

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DESCRIPTION OF PLATE

PLATE 2

Photomicrographs of meiosis and mitosis in anthers of *Lilium longiflorum*, 7μ; stained in Heidenhain's iron-alum haematoxylin; photographed with Leitz "Makam."

Figures 1 to 5—meiosis.

Fig. 1—Diakinesis bivalent, at least three chromonemata visible, × 1425; figs. 2 and 3—IM bivalent, side view, two foci, × 1425; fig. 2—four chromonemata visible in short arms; fig. 3—the two chromatids of each bivalent partner distinctly shown; fig. 4—IM, polar view, chromonematic structure apparent in all twelve bivalents, in some the four chromonemata visible, × 810; fig. 5—IA, showing network formed by the four chromonemata in each chromatid, × 1425.

Figures 6 to 15—mitosis.

Fig. 6—"Resting" nucleus, fixation somewhat coarse, parallel strands representing the two chromatids of a chromosome can be followed for short distances, four-strand structure (characteristic of less coarse fixation) occasionally visible, × 1350; fig. 7—early prophase, where approximation of strands within individual chromosomes with consequent breaking of anastomoses forms chromosome tracts in which four-strand network is evident, × 1350; fig. 8—late prophase, chromosome end showing separation of daughter chromonemata at extremity of one chromatid, × 1900; figs. 9 and 10—late prophase, two foci, chromomere-like structure of chromosome lying across equator in figure 10 results from beginning of separation of daughter chromonemata at points where anastomoses pull them apart as shown, at a later stage, in figure 9 lower left-hand corner, × 1350; fig. 11—late prophase, showing ladder-like stage, × 1080; figs. 12 and 13—late prophase, two foci of a chromosome shown in upper left of figure 11 (chromatic dots near middle identify this chromosome in figures 11, 12, and 13), note that each chromatid contains two chromonemata, × 1900; figs. 14 and 15—metaphase, two foci, end of a chromosome at lower left in figure 14 shows four parallel coiled chromonemata, two closely approximated in each chromatid, chromosome at lower right in figure 15 appears to contain a single coiled chromonema in right-hand chromatid but left-hand chromatid clearly shows two independently coiled chromonemata, × 1900.

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STUDIES IN NICOTIANA

II. A TAXONOMIC SURVEY OF THE AUSTRALASIAN SPECIES

BY

HELEN-MAR WHEELER

INTRODUCTION

Though long recognized as a highly variable assemblage extending from Western Australia to Polynesia, and already possessed of an extensive synonomy, all the indigenous Australasian species of *Nicotiana* have commonly passed under the one name, *Nicotiana suaveolens* Lehmann. This is not surprising when we consider, as has been pointed out by Setchell (1912), that even the American species, *N. acuminata* (Grah.) Hook., has at times been identified as *N. suaveolens.* Nevertheless, recent publications of Black (1926; 1933) describing two new species and Domin (1929) recognizing at least nine, both new and redescribed, clearly indicate that this treatment as a single polymorphic species is inadequate (cf. also Goodspeed, 1933). However the exact number of species recognized within a puzzling group may fluctuate with different taxonomic concepts, more precise organization is desirable.

The present survey, dealing with species occurring in Australia, Lord Howe Island, New Caledonia, Isle of Pines (Kounié), Loyalty Islands, and Tongatâbu, is based on data obtained from living plants growing in the University of California Botanical Garden and on information from herbarium sheets. Although necessarily incomplete because many of the species still are little known, it is hoped that the following systematic arrangement of the material now available on this geographically isolated group of the genus will prove of value. Figures are omitted since this material is being illustrated by Professor T. H. Goodspeed in his forthcoming monograph of the genus.

The basis of any classification of the Australasian members of the genus *Nicotiana* will, of course, be comparative morphology, but, inasmuch as morphological distinctions so often become obscure and intergrading in this group, it has seemed important to determine whether cytogenetics might not add significant information. Results of investigations at the University of California on chromosome number (cf. Goodspeed, *loc. cit.*) indicate that there is a group of 16-paired species in southeastern Australia, an 18-paired species in central Australia, a 20-paired extending from western New South Wales to southeastern Western Australia, another 20-paired in eastern Queensland, a 22-paired in southwestern Western Australia, and a 24-paired along or near the coast of Queensland and New South Wales, Lord Howe Island, and New Caledonia. Whereas North and South American representatives usually are

12- or 24-paired species, rarely 9- or 10-paired, there is here some indication that the Australasian species may constitute a distinct evolutionary line of the genus, the nodes of which are often characterized by distinctive chromosome numbers. Gigantism is in some instances accounted for by tetraploidy (cf. Goodspeed, as reported by East, 1928). Chromosome morphology and degree of compatibility between various species as reflected by behavior in hybridization and genetic analysis also promise definite contributions to inter- and, in *N. suaveolens,* intraspecific relationships. Indeed, one strain of this polymorphic species has already been partly reconstructed. Therefore, some weight has been given to available cytogenetic data in evaluating the significance of certain characters and the limits of some species. In this report, however, specific reference to the cytogenetic aspect of the problem of origins and relationships of the species considered has been confined to the noting of chromosome numbers and brief statements concerning segregation in certain of the garden cultures. Cytological and genetic studies now in progress will be reported elsewhere.

ACKNOWLEDGMENTS

The writer gratefully acknowledges the advice and encouragement of Professor T. H. Goodspeed and his generosity in permitting the use of his cultures and herbarium notes. She wishes also to thank Professor H. L. Mason and Mr. E. Cheel for many helpful suggestions.

MATERIAL

The material for the garden study, with the exception of one long-established strain, consisted entirely of accessions from known native localities, 18 in number.[1] In 1929, 5 species and 1 tetraploid race were grown; 2 species were added in 1931; 1 species and another tetraploid race in 1932; one species in 1933. Original populations in the field generally consisted of no less than 15 plants, usually 25, sometimes 50 or more. Subsequent generations were sometimes reduced as the strain on selfing became a pure line. The writer was particularly fortunate in being able to compare one Australian species with another throughout its course of development, and in having the opportunity to see what is probably the largest collection of American species of the genus growing near, and under the same conditions as the Australian.

Herbarium sheets personally examined numbered more than two hundred, and, through the kindness of Professor Goodspeed, these were supplemented by his notes or photographs of many others examined by him in foreign herbaria. So far as can be ascertained, the sheets studied represent a considerable portion of the specimens of Australasian *Nicotiana* available in large herbaria throughout the world, and include a number of the specimens sent in to Baron von Mueller. The following abbreviations are used in this paper to designate herbaria:

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[1] Professor Goodspeed's stocks, designated more specifically in the treatment of each species. Specimens from these cultures are being deposited in the University of California Herbarium under the accession and culture numbers.

B	Black (J. M., Adelaide)
Be	Berlin (Botanisches Museum)
BM	British Museum
D	Delessert (in Conservatoire et Jardin Botanique, Geneva)
G	Gray
K	Kew
M	Munich (Botanisches Museum)
P	Paris (Muséum d'Histoire Naturelle)
Q	Queensland Government
S	Stockholm (Kungliga Riksmuseum)
UC	University of California
US	United States National
V	Victoria National
Vn	Vienna (Naturhistorisches Museum)
W	New South Wales National
WA	Western Australia Government

The coöperation of the herbaria which gave opportunity to study this material is gratefully acknowledged.

Always, when material has been available for comparison, the picture of species from garden cultures has closely corresponded to that obtained from herbarium specimens coming from the same native locality.

SPECIAL MORPHOLOGY

Australasian species of the genus *Nicotiana* are shallowly rooted, rather slender-stemmed herbs a few centimeters to more than 1.5 meters high,[2] nearly glabrous to densely woolly, occasionally viscid, the inflorescences generally long, their axes and branches very slender. Certain structural features warrant special description. (Hereafter reiteration is confined, for the most part, to new species.)

Pubescence.—Four types of epidermal hairs occur:

(1) aciculate, a tapering filament of cells not terminating in any head;

(2) spheric-headed, a tapering filament of cells terminating in a spherical, unicellular head;

(3) ellipsoid-headed, a tapering filament of cells terminating in an ellipsoidal, multicellular head, the entire hair appearing more or less clavate;

(4) discoid-headed, a single, much elongated cell (occasionally two) terminating in a thick-discoid or cushionlike head with cells radially disposed at right angles to stalk of hair, the entire hair appearing more or less tack-shaped.

In every species there are at least a few hairs on bractlets, pedicels, calyx, corolla, and usually on first few leaves. Number of types, distribution, and modification of hairs are correlated in part with species, in part with such factors as organ and distance from base of plant. Aciculate hairs always occur in lower part of interior of corolla tube. Except for interior of corolla and semidepauperate condition of head of many hairs on exterior of corolla, general tendency is to produce fewer aciculate hairs and more capitate hairs from base of plant upward; commonly aciculate are absent by inflorescence. Transitional aciculate to spheric-headed types are frequent where both merge. Viscidity usually is associated with ellipsoid-headed hairs, rarely with other capitate types. Firm excrescences sometimes found on stems, pedicels, calyx, occasionally even on leaves, are caused by enlargement of one or more proximal cells of certain hairs (commonly spheric-headed) and accumulation of a brownish substance within; remainder of hair wears off; protuberance sometimes is further raised by cells adjacent to hair.

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[2] In measurements given of height of plant, width of stem near base, length and width of leaves, etc., in this paper, "to" indicates maximum measurement known to author, not necessarily the maximum of any one or even the average plant. More than one maximum is included only when the highest measurement appears definitely restricted to a particular strain. Classification into annual and perennial is intentionally avoided at this time.

Flower.—Fragrance, if any, nocturnal. Calyx distinctly lobed or cleft, colorless membranous strips usually present in tube, teeth usually subequal. Corolla salverform or subsalverform, frequently yellow or purplish in bud, commonly drying yellowish, tube slightly obconic near mouth,[8] or slightly swollen and subsequently a little contracted, or both, the outside rarely pure white, usually pale greenish, greenish cream, or commonly—either typically or in certain weather—purplish, very seldom glabrous, usually covered with fine, short (rarely long) hairs, inside pale greenish or greenish cream, prominently ribbed below stamen insertions (ribs extending to near base of corolla—these were aptly described by older authors as adnate parts of stamen filaments, but the practice was later discarded to avoid ambiguity), pubescent toward base, limb convolute-plicate in bud, loosely so in closing or dying, otherwise spreading, inner side glabrous and pure white, outer side puberulent to glabrate (rarely conspicuously pubescent), usually whiter than tube but also more or less cream, green, or purplish, shallowly 5-lobed, lobes equal or nearly so, only rarely distinctly unequal, broad and obtuse or slightly deeper and more distinctly rotund, usually emarginate, sulcate within, slightly carinate on outer side. Stamens included, four equal or slightly didynamous, their filaments slender, pale greenish, erect until incurved toward apex, their subrotund (rarely rather narrowly elliptic or elliptic-oblong) anthers reaching or near mouth of corolla tube, fifth stamen usually affixed lower, its filament frequently somewhat arcuate or arcuate-erect, its anther below other four anthers. Hypogynous disc conspicuous, pale orange to deep orange-red. Ovary pale green, style slender, pale greenish to white, stigma green, subdiscoid, sulcate, commonly slightly exceeding anthers.

Capsule.—Erect, submembranaceous, usually containing 100–300 seeds; dehiscence accompanied by some separation and inward contraction of partition from ovary wall, likewise some separation of valves from each other, septicidal scission never extending below middle, loculicidal scission usually less, four teeth thus produced commonly somewhat recurved.

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[8] "Mouth" restricted to point at which limb departs abruptly from tubular part of flower; "throat" so indistinct when present that it is treated here as dilation of tube immediately below mouth.

KEY TO SPECIES

- Inflorescence leafy; cauline leaves cordate or ovate ………… 1. *N. Benthamiana*
- Inflorescence bracteate; cauline leaves various, rarely cordate
  - Cauline leaves markedly decurrent on stem ………… 2. *N. excelsior*
  - Cauline leaves scarcely or not at all decurrent on stem
    - All stamens affixed in lower half of corolla tube; stem viscid above with ellipsoid-headed hairs ………… 3. *N. Debneyi*
    - Four of the stamens affixed near mouth of corolla tube (excepting certain strains of *N. maritima*); stem not viscid in most species
      - Cauline leaves linear-spatulate, few ………… 4. *N. fragrans*
      - Cauline leaves not linear-spatulate nor necessarily few
        - Cauline leaves sessile, at insertion broad or broadening
          - Plant viscid with ellipsoid-headed hairs ………… 5. *N. occidentalis*
          - Plant not viscid; at most, moist to touch ………… 6. *N. Gossei*
        - Cauline leaves not sessile, tapering toward insertion or with a more or less distinct or winged petiole
          - Corolla tube more than 50 mm. long;[4] lowest stamen affixed toward mouth of corolla tube ………… 7. *N. megalosiphon*
          - Corolla tube not more than 50 mm. long, frequently much shorter; lowest stamen affixed near or below middle of corolla tube
            - Corolla tube 3–5 mm. wide
              - Corolla tube 15–25 (rarely 30) mm. long, usually 1.5–2.5 times as long as calyx
                - Pubescence velvety; leaf petioles distinct, slightly or not at all margined; corolla tube width increasing slightly but not unilaterally as tube emerges from calyx ………… 8. *N. velutina*
                - Pubescence not velvety; leaf petioles indistinct or broad-winged; corolla tube width showing small unilateral increase as tube emerges from calyx ………… 9. *N. maritima*
              - Corolla tube 25–50 (rarely 20) mm. long, usually 3–3.5 times as long as calyx ………… 10. *N. suaveolens*
            - Corolla tube 1.5–2.5 mm. wide
              - Capsule at least 10 mm. long; corolla tube at least 20 mm. long
                - Capsule length 6 times its width; leaves pubescent ………… 11. *N. stenocarpa*
                - Capsule length not more than 4 times its width; leaves glabrous or nearly so ………… 12. *N. ingulba*
              - Capsule less than 10 mm. long; corolla tube commonly less than 20 mm. long
                - Pubescence conspicuous, hairs distinct, glistening ………… 13. *N. rotundifolia*
                - Pubescence inconspicuous or lacking
                  - Cauline leaves oblanceolate; habit grasslike, erect ………… 14. *N. Goodspeedii*
                  - Cauline leaves ovate- or elliptic-bladed; habit rather spreading ………… 15. *N. exigua*

DESCRIPTIONS OF SPECIES

1. **N. Benthamiana** Domin, Biblioth. Bot., 22:591, pl. 37, fig. 1, 1929.

N. suaveolens var. *cordifolia* Benth., Fl. Austr., 4:470, 1869.

Erect, more or less pubescent throughout with patent villose hairs (spheric- and apparently modified discoid-headed). Root slender, tap. Stem slender, branches few, high, short. Rosette absent or not persisting, cauline leaves numerous, to 8×3.5 cm., petiole barely margined, a few lower leaves with blade elliptic or elliptic-obovate, remainder cordate or broadly ovate, acute or subacuminate, entire, subundulate, main lateral veins distinct, upper leaves smaller, shorter-petioled, becoming sessile. Inflorescence little branched; leaves scarcely or only slowly reduced to bracts; pedicel shorter than calyx, later ca. equaling capsule. Calyx broadly subcampanulate, to 18 mm. long, teeth acute, about as long as tube. Corolla tube to 5–6 cm., very slender. Four stamens affixed near mouth of corolla, fifth affixed somewhat lower. Stigma barely exserted. Capsule ovate-elliptic, included. Seeds at least 0.5–0.6 mm. long, oval-triangular to suboblong, brown, rugose, ridges wavy, embryo bent.

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[4] Variant in Western Australia with corolla tube ca. 40–50 mm. long?

Western Australia: Northwest coast, *Bynoe,* TYPE (not seen, known from Domin's drawing); between Ashburton and Yule Rivers, *Clement* (*fide* Domin). Central Australia: 1883, Winnecke, 19 (V).[5]

Distinguishable from *N. suaveolens* by foliate inflorescence, large, broad calyx, and very slender corolla tube.

A little known but very distinct species, previously reported only from the northwest coast. Whether or not "Central Australia" proves valid as a locality, the striking resemblance of Winnecke's two small plants to Domin's drawing leaves no doubt they are *N. Benthamiana.* Leaf, flower, and calyx measurements in description above are from Domin's drawing and description. Note, however, that Bentham, citing only "N. W. coast, Bynoe," described *N. suaveolens* var. *cordifolia* as having "corolla of the common size (1–1½ in. long)." Bentham's only further characterization was "Leaves almost all cordate. Calyx large with broad lobes."

2. **N. excelsior** Black, Trans. Roy. Soc. S. Austr., 50:286, 1926.

N. suaveolens var. *excelsior* Black, Trans. Roy. Soc. S. Austr., 39:835, pl. 63, fig. 2 and pl. 70, 1915.

N. macrocalyx Domin, Biblioth. Bot., 22:593, pl. 36, figs. 9, 10, 1929.

To 2 m. high, nearly glabrous (few, short, conspicuous aciculate hairs scattered along leaf margins, swollen bases persistent there as are bases of spheric-headed hairs found on calyx; short spheric-headed hairs on exterior of corolla). Stems 1–several (6–8?), erect or assurgent, 15 mm. diam. near base, slowly decreasing upward. Leaves all cauline, sessile, decurrent on stem, oblong-elliptic to obovate, acuminate, to 30 × 10 cm. (exclusive of decurrent wings 2–12 cm. long), rather crassulate, main lateral veins distinct, margin undulate, often sparsely serrated with short firm points. Inflorescence occasionally forked, bracts soon small and subtriangular, often decurrent, pedicels 7–11 mm., later 10–16 mm. Flowers directed obliquely upward or subhorizontal, vespertine, slightly fragrant. Calyx subcylindric or slightly obconic, 20–30 mm. long, 10-ridged, membranes slender but conspicuous, teeth shorter than tube, acuminately prolonged. Corolla frequently purplish outside, tube 35–40 mm. long, narrower than calyx on emerging from it, ca. 4 mm. wide, gradually increasing at upper end until 6–7.5 mm. at mouth, limb 30–35 mm. across. Four stamens affixed near mouth, fifth affixed near middle of corolla tube, its anther 9–10 mm. below other anthers. Stigma barely exserted. Capsule shorter than or ca. as long as calyx. Seeds ca. 1 mm. long, subreniform-oblong, brown, honeycombed, ridges only slightly wavy, embryo bent.

South Australia: Mount Carmeena (Everard Range), Aug. 12, 1914, *White,* TYPE (B); Birksgate Range, July 11, 1891 (V,W) and July 12, 1891 (V), *Helms;* Ernabella (Musgrave Ranges), *Cleland* (B).

Distinguishable from *N. suaveolens* by decurrent leaves, long calyx; from *N. Gossei* by decurrent leaves, glabrousness.

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[5] "19" on separate slip. A similarly labeled sheet without number in same herbarium belongs to *N. ingulba* Black.

3. **N. Debneyi** Domin, Biblioth. Bot., 22:593, pl. 36, figs. 6–8, 1929.

N. suaveolens var. *parviflora* Benth., Fl. Austr., 4:470, 1869, as often interpreted.

Not *N. suaveolens* var. *Debneyi* Bailey.

To more than 1 m., rather minutely pilose throughout except for occasional subglabrous leaves, scabrous on stems, commonly scabridulous on leaves, especially midrib of lower side but often sparsely, minutely so over entire upper surface, viscidity commencing at or near inflorescence and extending through calyx (aciculate hairs at base of plant, spheric- and discoid-headed up to inflorescence, then ellipsoid- and few discoid-headed through calyx, ellipsoid-headed becoming more rudimentary on outside of corolla and there associated with aciculate and spheric-headed; excrescences involving bases of aciculate, spheric-headed, occasionally ellipsoid-headed hairs). Root tap or soon divided, frequently quite fibrous. Stems 1–several (initial stem usually well developed before outer stems appear), to nearly 1 cm. diam. near base, gradually tapered, distantly branched, seldom forked. Leaves coarse, thin or occasionally somewhat fleshy, to 23–35 cm. long and 8–13 cm. wide, margin frequently plane or nearly so, main lateral veins distinct, rosulate leaves few, semipersistent, spatulate-obovate to oblanceolate, obtuse or acute, cauline leaves auricled, obovate, oblanceolate, or a few even obcuneate, apex acute or acuminate. Inflorescence extensive, decompound, branches numerous, usually alternate, shorter and more slender than axis from which they depart, sometimes purplish, bracts sessile, acute, soon reduced to 2–3 mm., pedicels 2–6 mm., later 8–13 mm. Flowers more or less horizontal or slightly nodding, odorless, not vespertine. Calyx broadly tubular or subcampanulate, often purple-nerved or -tinged, 5–9 mm. long, membranes narrow, often indistinct, teeth slender, ca. as long as tube, sometimes unequal. Corolla frequently pink- or purplish-tinged on outside, sometimes glabrous, tube 15–21 mm. long, 2–2.5 mm. wide, usually gently arcuate and slightly angled, commonly broadest in region of stamen insertion, limb 8–12 mm. across, more or less diagonal by reflexing of 3 upper somewhat smaller lobes, erectness of 2 lower lobes. Four stamens affixed near or below middle of corolla tube, fifth affixed slightly lower and curved at base, its anther ca. 2 mm. below other anthers, anthers greenish yellow. Stigma at mouth or barely exserted, sometimes obconic. Capsule ovate or ovoid, 7–9 mm. long, equaling or exceeding calyx, septicidal scission to middle, loculicidal shorter. Seeds ca. 0.7–0.8 mm. long, oval or suboblong, brown (Ridgway's cinnamon-brown),[6] reticulate, ridges distinctly to broadly undulating, embryo straight. Chromosome number 24 pairs.

Eastern Queensland: Rockingham Bay, *Dallachy*, TYPE (not seen); Mount Maconnels, Nov. 18, 1843, *Leichhardt* (W); Rockhampton, Aug., 1912, *Boorman* (W); Gayndah, May, 1917, *White* (V, W). Eastern New South Wales: Near Lismore, Nov., 1911, *Tanner* (W); Hastings River (K); Paterson, Oct., 1929, *Rupp* (W); Kiama, Jan., 1856, *Harvey* (K). Lord Howe Island: Cultivated at Ashfield, N. S. W., from seed from Lord Howe Island, Nov. 24, 1929, *Cheel* (W). New Caledonia: 1862, *Pancher* (P, K); 1861, *Deplanche* 316 (P); Noumea, l'Anse Vata, *Franc*, Hb. Bonati 806 (K, Q, Vn, UC, W).

Distinguishable from *N. suaveolens* by distinctly auricled cauline leaves, viscid inflorescence, small nonvespertine flowers with lower stamen insertion; from *N. exigua* by viscidity, lower stamen insertion.

Domin's description characteristic of this widely distributed yet not highly variable species. Univ. Calif. Bot. Gard. accession 1928–1 (seed collected at Mount Johnstone near Paterson, N. S. W., *Rupp*) gave plants with blade of cauline leaves tapered into broadly winged "petiole," calyx 5–6 mm. long, corolla purple-tinged, tube to 17 mm. long, limb to 12 mm. across. In cultures derived from 1931–59 (mixed lot of seed collected at Dalby, Q., *McCarthy*, yielding also *N. megalosiphon* and *N. exigua*) leaves were larger, cauline frequently strictly sessile and auriculate by constriction of elliptic blade, calyx to 9 mm., corolla segregating for presence of purple, tube to 21 mm., limb to 10 mm. Accession 1932–48 (seed taken from *Cheel* sheet in Hb. N. S. W., cited above under Lord Howe Island) gave some very large-leaved plants but otherwise closely resembled 1928–1. All cultures hardy, leaf width highly variable, flowers sometimes small and depauperate on plants with many capsules matured.

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[6] For definition of any color specifically referred to Ridgway, cf. Ridgway (1912).

Ithaca Creek, *Fink* (Q), probably belongs to *N. Debneyi*, but in long pedicel and stamen insertion approaches *N. exigua.*

4. **N. fragrans** Hooker, Bot. Mag., t. 4865, 1855.
N. Macgillivrayi Seeman, Fl. Vit., 179, 1866.
N. suaveolens var. *macrantha* Comes, Monogr. Nicot., 41, 1899.

To over 1 m., shortly silky-pubescent throughout, subglutinous. Leaves fleshy, rosulate large, spatulate, to 15 cm. long, petiole very distinct, slender, 8.5 cm. long, blade broadly ovate, 6.5 × 3.5 cm., or rosulate leaves smaller, petiole less distinct, blade more oblong; cauline few, linear-spatulate. Inflorescence extensive, branched, smaller branchlets more or less congested, multiflorate, bracts inconspicuous, small, pedicels 8–15 mm., later 15–30 mm. Flowers pendent, fragrant. Calyx ovate, inflated, ca. ⅕–⅙ as long as corolla tube, membranes absent(?), teeth 5 or 6, no longer than tube, subulate, subequal or unequal. Corolla tube 55 to 90 mm. long, ca. 3–4 mm. wide, more slender toward base, conspicuously but gradually broadening near mouth, limb to 70 mm. across, lobes 5 or 6. Stamens 5 or 6; 4 affixed near mouth, fifth also affixed in upper half of tube, its anther slightly below other anthers. Stigma at mouth or barely exserted. Capsule rotund-ovate, included.

Isle of Pines (Kounié): Oct., 1853, *MacGillivray* (K, BM), *Milne* (K), TYPE locality, both collectors cited by Hooker. Loyalty Islands: *Grey* (K); Lifu, *Whitmer* (BM), *Veillard* 1030, collected by *Deplanche* (P). Tonga: Island Tongatábu, south coast, *Graeffe* (K).

Distinguishable from *N. suaveolens* by persistent indument, longer flowers; from *N. megalosiphon* by few linear-spatulate cauline leaves, pendent flowers; from most long-tubed Australian species by short broad calyx.

Smaller, more oblanceolate leaves in specimens from the Loyalties and Tongatábu and possibly shorter corolla tube (Tongatábu sheet lacks flowers) may prove of varietal significance. Stout base of Tongatábu sheet suggests Comes's *N. suaveolens* var. *tuberosa*. Exact situation of stamens known only for Lifu sheet cited, in which filament of fifth stamen is 6 mm. long and its anther 3–4 mm. below other anthers.

5. **N. occidentalis** sp. nov.

Herbacea, viscido-pubescens; foliis cauliniis inferis ovatis lanceolato-ovatisve, acutiusculis, prope basim angustatis dein subauriculatis dilatatis, superis ovato-acuminatis obcuneatisve, sessilibus, subamplectentibus; inflorescentia laxe ramosa, bracteis evidentibus; corollae hypocraterimorphae tubo calyce 3–5–plo longiore, limbi lobis obtusis, emarginatis; staminibus in tubo corollae inclusis, 4 prope orificium affixis, quinto prope medium tubi affixo, anthera sua ceteris supposita.

2–4.5 or more dm., shortly viscid-pubescent (ellipsoid-headed hairs predominant, other hairs scarce, some spheric-headed toward base of plant, also on exterior of corolla, aciculate on interior of corolla tube; discoid-headed not well developed [?]). Stems 1–several, to 6 mm. diam. near base, much slenderer above, erect or ascendent, forking. Rosette leaves usually not persisting(?), commonly few, spatulate or elliptic subpetiolate. Cauline leaves numerous, sometimes lowest subspatulate, auriculate, otherwise all sessile, more or less clasping, to 11 × 3 cm., main lateral veins apparently rather obscure, lower leaves ovate- or broadly lanceolate-subpandurate, upper attenuate from broadish base. Inflorescences terminal or axillary, lower limits indistinct, even slender, lanceolate upper bracts frequently 18 mm. long and dilate-based, pedicels 5–9 mm., later 7–14 mm. Flowers erect or directed obliquely upward, occasionally cleistogamous(?). Calyx subcampanulate, 9–10 mm. long, membranes narrow but conspicuous, teeth rather slender, shorter than tube. Corolla subsalverform, in sicco whitish or cream, tube 25–50 mm. long, 2–2.5 mm. wide, near mouth gradually dilated to 4–5 mm., ribbed inside below stamen insertions, limb ca. 30 mm. across, lobes shallow, obtuse, sulcate, emarginate. Stamens included, 4 affixed near mouth of corolla tube, fifth in upper half of tube, its anther ca. 5–6 mm. below other anthers. Stigma barely exserted. Capsule ovate-ellipsoid, 10–12 mm. long, equaling or exceeding calyx, loculicidal and septicidal scission short. Seeds dark brown, 0.7–0.8 mm., rotund-reniform, surface honeycombed, ridges rather straight, embryo bent.

Western Australia: Bezout Island, Voyage of Beagle, 39–40, *Wickham* and *Stokes* (BM); Port Hedland, Aug. 11, 1911, *Mjöberg* 105, TYPE (W), topotype? (S); near Mount Hale, 1884, *Crossland* (V); near Lake Austin, 1886, *King* (Be, US); Champion Bay, Sept., 1899, *Crawford* (WA); Greenough near Geraldton, Oct., 1898, *Helms* (W); Mount Burges, 1860 (K).

Distinguishable from *N. suaveolens* by viscid indument and sessile, subpandurate to obcuneate cauline leaves.

Tendency to cleistogamy suspected (type sheet); subdidynamy of 4 upper stamens noted (Champion Bay sheet). Closely resembling *N. occidentalis*, possibly merely variants of it, are collections from Yuin, 1888, *Hy*— (V) and between Northampton and Shark Bay, 1884, *Carey* (V), both with corolla tube ca. 30 mm. long, slightly and gradually increasing from calyx upward, limb broad, latter specimen with some bracts subovate; between Ashburton and De Gray Rivers, *Clement* (K), corolla tube ca. 20 mm. long, limb short; near Roebourne, Aug., 1884, *Carey* (V), corolla tube ca. 15 mm. long, capsule more slender than species, the patent, ellipsoid-headed hairs distinct, conspicuous, inflorescence rather extensive, its lower limit well defined.

6. **N. Gossei** Domin, Biblioth. Bot., 22 :592, pl. 36, figs. 2–5, 1929. Black, Trans. Roy. Soc. S. Austr., 57 : 155, 1933.

Coarse, to 1 m., conspicuously pilose to woolly, sometimes moist to touch (aciculate hairs from base of plant to or into inflorescence, reappearing on corolla, discoid-headed increasing upward, through calyx, spheric-headed in inflorescence, tending to revert to aciculate on exterior of corolla). Stems to 15 mm. diam. near base, rather stout to inflorescence. Leaves cauline, numerous, coarse but usually not fleshy, sessile (few rarely subpetiolate), to 20 × 11 cm., main lateral veins distinct, margin plane or subundulate, lowest spatulate or obovate, obtuse, middle broadly pandurate or subpandurate, semiclasping, recess usually shallow, short, sometimes prolonged, apex acute, upper becoming ovate to broadly oblong, apex acute, acuminate, or submucronate, uppermost triangular attenuate. Inflorescence rather short, branching, frequently more or less congested and flat topped, multiflorate, capsules proximate, even upper bracts 10 mm. long, triangular-attenuate, pedicels 3–10 (rarely 18) mm., later 8–15 mm. (rarely longer). Flowers directed obliquely upward or almost erect. Calyx tubular, 15–25 mm. long, 5-ridged, membranes frequently indistinct, teeth linear-lanceolate, subequal to tube. Corolla tube often purplish outside, 40–60 mm. long (late season as low as 22 mm.), 3–4 mm. wide, obscurely trumpetform, limb ca. 25–30 mm. across. Four stamens affixed near mouth of corolla tube, fifth affixed above or near middle of tube, its filament 6–15 mm. long, its anther 5–12 mm. below other anthers. Stigma at mouth or exserted. Capsule ovate-oblong, ca. 12–15 mm. long, included. Seeds 0.8–0.9 mm. long, brown (Ridgway's hazel), suboblong with one side somewhat concave, or broadly oval, reticulate, ridges wavy, embryo bent. Chromosome number 18 pairs.

Central Australia: "Centre of South Australia," *Gosse* 243, TYPE (not seen); north of Alice Springs, 1882, *Flint* (V); Mount Liebig, Aug., 1932, *Cleland* (B, UC); Finke River, 1882, *Kempe* (V); Hermannsburg, 1906–08, *Strehlow* (Be). Northern South Australia: Near Ernabella in Musgrave Ranges, Aug., 1933 (B).

Distinguishable from *N. suaveolens* by indument and large, broadly pandurate or subpandurate leaves; from *N. maritima* by broad, dilated leaf base, corolla tube length and shape; from *N. excelsior,* which may be its closest relative, by pubescence, leaves not decurrent on stem.

Tendencies toward *megalosiphon*-like corolla and stamen insertion, and *maritima*-like leaves most distinct trends noted. Although morphological and geographical limits not known, species appears concentrated in region cited above, with Lake Eyre, S. A., Sept., 1903, *Spencer* (W) and Mount Lyndhurst, S. A., May, 1898 *Koch* (K) suggesting possibility of southward extension and polymorphy. Certain of Koch's other collections from Mount Lyndhurst, however, are difficult to harmonize.

7. **N. megalosiphon** Heurck & Muell. Arg., *in* van Heurck, Obs. Bot., 126, 1870.

N. suaveolens var. *longiflora* Benth., Fl. Austr., 4:470, 1869.

To over 1 m., short, close, persistent indument throughout, becoming scabrid in inflorescence branches (sometimes stem more or less scabrid from base of plant) and calyx (hairs spheric- and discoid-headed except for aciculate on interior of corolla and possibly few on its exterior; excrescences chiefly from spheric-headed). Root tap to fleshy fasciculate. Stems 1–several, oblique or suberect, sparsely branched, occasionally forked, to 1 cm. diam. at base, decreasing until slender. Basal leaves few, spatulate, to 11 × 5 cm., forming rosette in young plant only, cauline leaves numerous, usually not fleshy, to 16 × 9 cm., petiole winged, base frequently somewhat auriculate, blade ovate, lanceolate-ovate, or triangular-attenuate, apex barely acute to markedly acuminate, rarely submucronate or obtuse, margin variable, main lateral veins distinct. Inflorescence long, branching variable, commonly little, sometimes by forking, bracts appressed, slender lanceolate, even uppermost bracts often 10–15 mm., pedicels 5–20 mm., later 12–30 mm. and 3–5 cm. apart, buds few. Flowers erect or suberect, vespertine, fragrance delicate and similar to that of cultivated petunia. Calyx narrowly campanulate or tubular, 10–20 mm. long, 10-ridged, membranes prominent, teeth slightly unequal, slender, tapering, ca. as long as tube. Corolla sometimes pink or purple-tinged outside, tube 60–90 (in late season as low as 40) mm. long, 1.5–2.5 mm. wide, conspicuously uniform except for slight dilation near mouth, limb 25–40 mm. across. Four stamens affixed to corolla tube near mouth, fifth affixed in upper half of tube, its filament 1–7 mm. long, not observed to curve, its anther from almost as high as other anthers to 4 mm. below them, anthers purple, purple-tinged, or greenish yellow. Stigma at mouth or barely exserted, 1–4 mm. above anthers, subdiscoid. Capsule bluntly slender-ovate, 11–15 mm. long, shorter than or ca. equaling calyx, septicidal split deep, loculicidal shorter. Seeds 0.9–1.0 mm. long, brown (Ridgway's cinnamon-brown), oblong-arcuate with one side somewhat concave, honeycombed, ridges nearly straight, embryo bent. Chromosome number 20 pairs.

Eastern Queensland: (Toward coast sometimes associated with *N. Debneyi.*) "... ad Portum Curtis (hb. van Heurck, collector ignotus probabiliter Damell)" van Heurck and Müller, TYPE (not seen); near Maconnels, Nov. 18, 1843, *Leichhardt;* Moreton Bay, *Mallard* (G); Blackall, May, 1880, *Ranking* (Q); Charleville, Sept., 1920, *Turner* (Q); Chinchilla, March, 1909, *Maiden* (W); Curriwillighi, 1868, *Dalton* (K). New South Wales: Bellata, Feb., 1920, *Roberts* (W); Narrabri, Nov., 1899, *Maiden* (W).

Distinguishable from *N. suaveolens* by persistent indument, corolla tube long, slender, and uniform in width, filament of lowest stamen always short.

Relationship to *N. megalosiphon* of shorter-flowered specimens (usually with filament of lowest stamen 5–7 mm. long) on southern border of range, and of shorter-flowered (30–45 mm.), subpetiolate, nonauriculate-leaved, sparsely pubescent ones from Minilaya (*Forrest,* 1882, V), Gascoyne (*Forrest,* 1882, V), and Wooramel (*Robinson,* 1889, V), Rivers, W. A., is not clear. Plants grown from Univ. Calif. Bot. Gard. accession 1931–59 (seed collected at Dalby, Q., *McCarthy*) had stem scabrid from base and anthers purple; it segregated for leaf shape and orientation, length and width of corolla tube, and gave one plant with sterile anthers. Plants from 1933–1 (seed collected on Bowen River, 50 miles southwest of Bowen, Q., *Pollock*) were not scabrid until ultimate branchlets of inflorescence, had greenish yellow anthers, and segregated for degree of pubescence and unusually low, semipistalloid anthers.

8. **N. velutina** sp. nov.

Herbacea, velutina, subviscida; foliis petiolatis, laminis lanceolatis, ovato-lanceolatis, aut ellipticis; inflorescentia longa, laxe ramosa; floribus vespertinis, fragrantibus; corollae hypocraterimorphae tubo vulgo 1.5–2.5-plo calyce longiore, limbi lobis obtusis, emarginatis; staminibus in tubo corollae inclusis, 4 prope orificium tubi affixis, quinto infra medium tubi affixo, anthera sua circa 2 mm. antheris ceteris supposita.

Few dm. to ca. 1 m., dulled throughout by moist, viscid, whitish, velvety indument (short spheric- and discoid-headed hairs from base of plant through calyx, few aciculate hairs at base of stem and within lower part of corolla tube, spheric-headed or subaciculate on exterior of corolla). Root tap or soon divided into laterals, semirigid. Stems 1–many, to 1 cm. diam. near base, slender above, erect or assurgent, forking or with continuing axis and ascendent branches. Leaves chiefly in rosette or cushion in young plants, later only clothing stems, to 20 × 5 cm., somewhat crassulate, petiole well defined, little or not at all margined, blade elliptic-obtuse to broadly lanceolate, tapered at base, margin frequently undulate or revolute, main lateral veins fairly distinct, occasionally obscured on upper surface. Inflorescence long, loosely forked or with oblique branches from percurrent axes, capsules proximate, bracts inconspicuous, sessile, acute, ca. 4 mm. long, pedicels 7–11 mm., later 11–18 mm. Flowers directed obliquely upward, horizontal or slightly nodding, vespertine, honeylike odor similar to *N. suaveolens.* Calyx subtubular, 8–12 mm. long, intersepal membranes narrow, teeth slender, acute, subequal, as long as or distinctly shorter than tube, tips sometimes slightly recurved. Corolla salverform, tube 14–22 mm. long, ca. 3 mm. wide, commonly broadening to width of calyx on emerging from it, later often slightly decreasing again, faintly swollen near mouth, slightly contracted at mouth, outside cream, greenish, or purplish, inside pale green and ribbed below stamen insertions, limb 10–12 mm. across, convolute-plicate in bud, loosely so during day and on fading, otherwise patent, perpendicular to tube or slightly diagonal, within white, outside more or less whitish but often with flush of yellow, green, or purple, and green- or purple-nerved, shallow lobes nearly equal, obtuse, emarginate, sulcate. Stamens included, 4 affixed near mouth of corolla tube, fifth affixed below middle of tube, its anther several mm. below other anthers, filaments pale greenish, fifth somewhat arcuate, anthers elliptic-oblong, greenish yellow, sometimes purplish. Disc bright orange-red. Ovary ovoid, pale green, style pale green, stigma at mouth, slightly exceeding anthers, green, thick subdiscoid or slightly obconic, sulcate. Capsule narrowly ovate to subelliptic, 8–10 mm. long, about equaling calyx, septicidal split commonly 2–3 mm., loculicidal shorter. Seeds rotund-reniform, 0.7–0.8 mm. long, brown (Ridgway's hazel), rugose, ridges wavy, embryo bent. Chromosome number 16 pairs.

South Australia: Warrina, May, 1891, *Helms* 33 (V); between Stokes Range and Cooper's Creek, *Wheeler* (V); Petermorrow Springs, Sept., 1916, *White* (B). Southern Queensland: Between the Paroot[7] and Grey Range, 1881, *Morton* (V). New South Wales: Tibooburra, April, 1913, *Cronch* (W); Toorale-Goonery, Oct., 1912, *Boorman* (W); Cobar District, June, 1921, *Reuss*, "Grows Darling River country, mainly on red soil" (W); Wilcannia, Sept. 25, 1915, *Johnstone* (W); Broken Hill, Oct. 4, 1920, *Morris*, TYPE (W).

Meaning of "corolla long" in following notation pasted on type folder—"420. Small, slender plant, strong smelling, lower leaves large, flower greenish white, corolla long. May be *Nicotiana suaveolens.*"—is not clear in light of New South Wales Herbarium label determination as "*Nicotiana suaveolens* var. *parviflora* Bth." and size of flowers (not exceeding 22 mm.) in specimen. Marked genetic and seasonal variation in corolla length is common in *Nicotiana* species, however, and even slight increase in length in somewhat slender-tubed species makes the corolla tube relatively long.

Culture from 1931–60 (seed collected 60 miles east of Broken Hill, N. S. W., *Morris*) showed much variation in height, leaf size, and margin. Outdoors, corolla (14–18 mm. long) frequently developed purple on outside of tube and limb; in greenhouse, no purple. Hardy new shoots continued to spring from base after free flowering checked by cold. Crowding of buds and flowers on tips of young vigorous shoots in this culture indicates that occasional massing of open flowers may be expected.

9. **N. maritima** sp. nov.

Herbacea, albido-villosa usque ad subglabratam; foliis cauliniis obovatis, subsessilibus, aut laminis ovatis et in petiolos late-alatos contractis; inflorescentia longa, a latere diffundenti; floribus vespertinis fragrantibus; corollae curtae hypocraterimorphae tubo 1.5–2.5-plo calyce longiore et supra calycem a uno latere tumescenti, lobis corollae subrotundis, emarginatis; staminibus in tubo corollae inclusis, 4 aut prope orificium tubi aut prope medium tubi affixis filamentis usque ad orificium extensis, stamine quinto infra medium tubi affixo, anthera sua circa 2 mm. antheris ceteris supposita.

Few dm. to more than 1 m., densely white-villose to only obscurely pubescent, somewhat moist to touch (aciculate hairs extending from base of plant nearly to or into pedicels, reappearing on exterior and interior of corolla, spheric- and discoid-headed occasional below, increasing upward, latter disappearing on corolla, in some strains spheric-headed hairs forming harsh excrescenses from inflorescence rachis through calyx). Root tap or soon divided into rather fleshy or distinctly fibrous system of laterals. Stems 1–6, to 15 mm. diam. near base, slowly decreasing until slender, erect to spreading-assurgent, branched, sometimes forked. Leaves coarse, rather fleshy, lowest spatulate, obtuse, to 30 × 12 cm., distinctly rosulate in young plant only, cauline leaves many, often as large or larger, broad-obovate, or subpetiolate and broadly winged to insertion, wings sometimes slightly decurrent, blade ovate to elliptic, obtuse to acuminate, main lateral and often lesser veins distinct, margin undulate to finely crisped. Inflorescence extensive, paniculiform, occasionally forking, branches frequently long and spreading, buds on young inflorescences massed, capsules proximate, bracts lanceolate to subulate, appressed, rapidly reduced to 5 mm., pedicels 4–20 mm., later 13–25. Flowers directed obliquely upward or subhorizontal, vespertine, heavy honeylike fragrance as in *N. suaveolens.* Calyx tubular or campanulate, 10–20 mm. long, sometimes purplish, 5-ridged, membranes conspicuous wedges, teeth subequal, tapered, shorter than or ca. as long as tube. Corolla salverform, tube 15–30 mm. long, increasing unilaterally as it emerges from calyx until 3–5 mm. wide (as wide or wider than calyx tube), then uniform until near mouth, there faintly swollen and subsequently slightly contracted, greenish cream, the outside often purplish, inside ribbed below stamen insertions, limb 15–25 mm. across, convolute-plicate in bud, loosely so during day and on fading, otherwise spreading, frequently more or less diagonal to tube (upper lobes reflexing, lower oblique-erect), sinuses commonly extending inward halfway to mouth of tube, lobes subequal, obtuse, emarginate, sulcate, within white, outside green-nerved, tinged with yellow, sometimes with purple. Stamens included, 4 affixed near mouth or near middle of corolla tube, fifth affixed near middle, its anther ca. 2 mm. below other anthers, filaments pale greenish, the fifth arcuate, anthers subelliptic, greenish yellow or purplish. Disc deep orange-red. Ovary broadly ovoid, pale green, style pale green, stigma green, subdiscoid, sulcate, to 2 mm. above or almost even with anthers, scarcely exserted. Capsule elliptic to subglobose, 8–10 mm. long, subequal to calyx, septicidal scission several mm., loculicidal commonly less. Seeds subreniform, frequently angular, 0.8–1.0 mm. long, brown (Ridgway's hazel), more or less honeycombed, ridges nearly straight, embryo bent. Chromosome number 16 pairs.

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[7] Paroo River?

Coastal. South Australia: Coffins Bay (V); Port Augusta, Dec. 14, 1885, *Lea* (BM); Georgetown, 1893, *Richards* (V); near Adelaide, 1898, *Cleland* (W); University of California Herbarium 519502, Hallett's Cove (about 16 miles south of Adelaide), Sept., 1932, *Cleland*, TYPE (UC); banks of the Torrens, *Whittaker* (K). Victoria: Port Philippi,[8] *M.* (V).

Distinguishable from *N. suaveolens* by short corolla tube unilaterally increasing on emerging from calyx, usually also by deeper incised, diagonally spread limb; from *N. velutina* by longer, never viscid hairs, winged or indistinctly petiolate leaves, corolla tube shape; from *N. Gossei* by long spreading inflorescence, length and shape of corolla tube.

Cultures grown from Univ. Calif. Bot. Gard. accession 1933–2 (seed collected at the type locality, *Cleland*), were silvery white villose throughout, frequently woolly, on under surface of leaves tomentulose, corolla tube to 21 mm. long, limb to 21 mm. across, four upper stamens affixed near mouth of corolla tube; from 1932–4 (seed collected at Rosetta Head, S. A., *Cleland*), much less pubescent even when young, corolla tube to 19 mm. long, limb to 21 mm. across, four upper stamens affixed near mouth or toward middle of corolla tube; from 1927–9 (seed collected at Victor Harbour, S. A., *Osborn*), young plants and shoots dense white-woolly, at maturity hairs short, inconspicuous, leaves corrugated by main lateral veins, corolla tube to 17 mm. long, limb to 22 mm. across, four upper stamens characteristically affixed near middle of tube but in late season sometimes higher, tendency to 1–2 additional corolla lobes, stamens, ovary cells.

10. **N. suaveolens** Lehmann *in* Isis (von Oken), an. 1818, col. 36; Lehm., Gen. Nicot. Hist., 43, no. 18, 1818.

N. undulata Vent., Jard. Malm., t. 10, 1803. Sims, Bot. Mag., t. 673, 1803. Jacquin, Fragm. Bot., no. 155, t. 56, 1809. Not *N. undulata* R. & P.

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[8] Specimens and garden cultures suggest segregants of hybridization with *N. suaveolens* in or near this region.

N. Australasiae R. Br., *in* Tuckey, Narrative Exped. Expl. R. Zaïre, etc., Append. V:472, 1818.

N. vincaeflora Lag., Cat. Hort. Matrit. ex Link, Enum. Hort. Berol., 1:179, 1821.

N. suaveolens var. *undulata* (Vent.) Comes, Monogr. Nicot., 41, 1899.

N. suaveolens var. *vincaeflora* (Lag.) Comes, Monogr. Nicot., 42, 1899.

To 17 dm., frequently nearly glabrous or glabrate, sometimes minutely pilose or young shoots even white-villose (spheric-headed hairs most common, aciculate hairs confined to base of plant and seldom persisting, discoid-headed increasing upward but lacking on corolla). Root tap or soon divided into numerous fleshy laterals. Stems 1–8, to 10 mm. diam. near base in some strains, frequently forking. Basal leaves contributing to rosette, cushion or buttress, fleshy, spatulate or oblanceolate, subobtuse to acute, to 26 × 7 cm., sometimes to 38 × 14 cm., upper leaves smaller, more remote, winged "petiole" shorter and sometimes better defined, apex acute to acuminate, margin commonly somewhat undulate to finely crisped, main lateral veins fairly to quite distinct. Inflorescence long, seldom decompound, usually loosely forking, sometimes racemose branching more prominent, bracts linear-lanceolate to subulate, soon reduced to ca. 4 mm., buds few, pedicels 2–15 mm., later 10–20 mm. Flowers nearly horizontal or nodding, vespertine, fragrance heavy, sweet, honeylike. Calyx tubular-campanulate, occasionally purple-tinged, 9–16 mm. long, usually 5-ridged, membranes narrow, rather conspicuous, teeth subequal, slender, ca. as long as tube. Corolla often more or less purplish outside, tube 20–46 mm. long, 3–4 mm. wide, often slightly narrower within calyx, gradually broadening near mouth, limb 19–44 mm. across (commonly somewhat less than tube length), horizontal or only slightly diagonal. Four stamens affixed near mouth, fifth commonly affixed in lower half of corolla tube, sometimes in upper half, in either event its anther 4–6 mm. lower than other anthers, anthers commonly purple. Stigma typically exserted 1–4 mm., in late season at mouth and scarcely exceeding anthers. Capsule narrowly obtuse-ovate, ca. 10 mm. long, exserted or included, septicidal scission nearly to middle, loculicidal often nearly as far. Seeds 0.7–1.2 mm. long, reniform or angular subreniform, brown (Ridgway's hazel), clearly honeycombed to subrugose-honeycombed, ridges straight or somewhat wavy, embryo bent. Chromosome number 16 pairs and 32 pairs.

Eastern New South Wales: Moonan Brook, near Scone, 1883, *Carter* (V); Bully Island, Lake Macquarie, Nov. 24, 1929, *Cheel* (W); Jenolan Caves, Oct., 1899, *Blakely* (UC, US, Vn, W); Burrinjuck, Feb., 1911, *Boorman* (W). Victoria: Snowy River, *Mueller* (BM); Bacchus Marsh, March, 1857, *Wilhelm* (V).

Distinguishable from other Australasian species by no one character but by a combination of characters: nonviscid, generally only slight pubescence, semipetiolate cauline leaves, corolla tube 3–4 mm. wide, seldom less than 3–3.5 times as long as calyx, commonly 30–45 (extremes 20–50) mm. long, lower stamen usually affixed in lower half of corolla tube, its anther always ca. 4–5 mm. below other anthers.

Since the specimen "*Nicot. suaveolens*, Herb. Lehmann" (V) is undoubtedly the same species as "*N. undulata* ex Hortus Malmaison, Herbier de Ventenat" (D), and since Lehmann specifically states the change in name was necessitated by preoccupation of *N. undulata*, Ventenat's specimen may be assumed to be the type of *N. suaveolens*. His culture was from "graines envoyées d'Angleterre par M. le Chevalier Banks, Président de la Société royale de Londres, et Associé étranger de l'Institut National de France," the original locality for which was "du port Jackson." According to Ventenat's description and figure, the stem is "velue dans sa moitié inférieure, presque glabre dans la supérieure"; leaves "parsemées sur chaque surface, et principalement sur les nervures, de poils courts, molles, douces au toucher," rosulate spatulate, 14 × 5 cm., "festonées," cauline to 9 × 3 cm., "ovales, pointues, ondées sur leurs bords," all but the nearly sessile uppermost leaves contracted into sharply demarcated, winged petiole, blade corrugated by main lateral veins, apex acuminate; flower "d'un blanc de lait, répandant une faible odeur de jasmin, longues de cinq centimètres, larges de trente-quatre millimètres."

Though both Sims and Jacquin accepted Ventenat's name, *N. undulata,* their excellent descriptions and figures (showing cauline leaves indistinctly petiolate, lanceolate-acute, surface not corrugated, corolla lobes clearly emarginate, so broad as to make limb undulate) early extended the picture of strains apparently derived from type locality seed and possibly still growing in botanical gardens today. Certainly the University of California stock strain (received from E. M. East, Bussey Institute, U. S. A., who in turn had received it from R. Istituto Sperimentale Tabacchi, Scafati, Italy) is, except for being much less pubescent, remarkably similar to that of Sims and Jacquin.

Other synonyms cited above are accepted on the following grounds. *N. Australasiae* was specifically stated by Brown to be "the *N. undulata* of Ventenat and Prodr. Nov. Holl." As nearly as can be checked, Brown's name was published later than Lehmann's name, *N. suaveolens. N. vincaeflora* is said by Link to be "Valde affinis praecedente[9] ut differt caule glabro, superne praesertim asperiusculo." The stem in *N. suaveolens* usually retains pubescence, if at all, only toward its base and at tips of branchlets; harshness in ultimate inflorescence ramifications is common. Many old sheets determined as *N. vincaeflora* are *N. suaveolens. N. suaveolens* var. *vincaeflora* is based on *N. vincaeflora,* as *N. suaveolens* var. *undulata* is on *N. undulata.*

At present the writer recognizes no varieties. Var. *undulata* Comes, defined by Comes as "Planta elatior, fol. magis undulatis; flor. maioribus" is rejected because it includes Ventenat's concept of *N. undulata* and, therefore, the type form of *N. suaveolens.* Other varieties hitherto proposed have been indistinctly defined or based on so broad a conception of the species as to be unreliable. Moreover, the common scarcity of capsules in diploid cultures and herbarium sheets, necessity of hand-pollination in obtaining pedigreed seed, heterogeneous nature of cultures from the wild, and ease with which hybrids are obtained with neighboring species all point to the futility, in a species favoring cross-pollination, of naming a variation, unless it is clearly warranted and the form is readily recognizable from both living and pressed material. The following categories, an orderly arrangement of Univ. Calif. Bot. Gard. lines, cited by seed accession numbers, illustrate types of variation:

1. Large-flowered diploid—corolla tube 35–46 (usually 40–45) mm. long, limb 25–45 (usually 35–40) mm. across. (a) Univ. Calif. stock strain (1914–174, received from E. M. East), stems and leaves dark green, glabrous save

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[9] *N. undulata* Vent.

for few scattered hairs of young seedling, rosette persistent, few-leaved, loose, merged with lower cauline leaves; corolla predominantly ivory on outside, tube 40–45 mm. long, limb 27–44 mm. across, capsule included. (b) 1927–3 (seed from Burragorang Valley, N. S. W., through Sir Arthur W. Hill), stems and leaves light green, sparsely pubescent, leaves conspicuously thin, commonly somewhat rhombiform, frequently nearly all contributing to dense cushion or buttress, ultimate branches of inflorescence often scabridulous, corolla slightly funnelform, ca. as large as (a), tube purple outside, segregating for purpling of leaf, stem, and calyx.

2. Small-flowered diploid—corolla tube 20–35 (usually 25–33) mm. long, limb 19–33 (usually 22–30) mm. across. (a) 1927–7, 1927–10 (seed collected at Jenolan Caves, N. S. W., *Setchell*), subglabrous plants with herbage and calyx frequently purple-tinged, segregating for: size; vigor; leafy base little developed or leafy base forming dense mat or cushion below inflorescence (the very short leafy axillary shoots, "axillary rosettes," common in *N. suaveolens* particularly numerous in this strain); stems suberect or radiately spreading; leaves small or large (to 30 cm. long), patent or convex as if held by abnormal tensions, shortly subpetiolate-ovate and barely acute or longer subpetiolate-lanceolate (or oblanceolate) and much tapered at both apex and base, margin nearly plane or much undulate, surface plane or puckered; corolla tube 27–35 mm. long, limb 24–33 mm. across, lobes barely emarginate (occasional lobe unnotched) or distinctly so; capsule included or exserted. (b) 1927–8 (seed from Rowsley, V., through Sir Arthur W. Hill), subglabrous (though herbarium sheets indicate pubescent plants in Melbourne region), few-stemmed, sprawling, to 8–10-stemmed, erect, 15 dm. high, with bunchy, very leafy bases or leaves few and more distant; leaves slender lanceolate, plane, dark green, small, to broad-ovate, rugose, light green, large (35 × 12 cm.); corolla seldom at all purplish, tube 20–32 mm. long, limb 19–29 mm. across, 4 longer stamens with filaments very short to as much as 5 mm. long, anthers sometimes green.

3. Tetraploid—to 14–17 dm. (maximum height surpassing maximum height of all diploid cultures), stems thicker than diploids, leaves to 38 × 14 cm., capsules freely set. (a) 1927–2, 1931–36 (seed collected at Bathurst, N. S. W., second collection by *May*), strikingly slow to blossom, suggesting, save for flower size (corolla tube 35–41 mm. long, limb 25–34 mm. across), a giant *N. suaveolens* qualitatively similar to 1927–3 except for leaf more elliptic-ovate than rhombic-attenuate and shortly pubescent on under surface, young stems distinctly pubescent. Segregated for vigor, size of plant, insertion of lowest stamen (from low in tube, filament long, to high and filament short), purple and full vs. green and shrunken anthers. Most frequent teratological variation the appearance of a weaker membranous wedge which, if it splits, continues one interpetal sinus inward. Whereas *N. suaveolens* is variously listed as an annual or perennial, and even diploids appear to have sufficient vigor to overwinter under favorable conditions, mature tetraploid plants which arose as adventitious buds on roots of plants of the previous year were actually observed in this strain. (b) 1932–51 (seed taken from Lake Maquarie

sheet cited above), slower growing than some diploids but maturing much more rapidly than Bathurst tetraploids, sometimes dense white villose in lower half of young plant or on young shoots, stems glabrate above, leaves glabrescent or at least becoming inconspicuously short-pubescent, not tending to crowd toward base, but clothing stems to considerable height, inflorescence branches closer-spaced, less forking than other *N. suaveolens* cultures, corolla tube 32–35 mm. long, limb 23–27 mm. across. The short, sharply defined, narrow-winged petiole suggests Ventenat's strain.

11. **N. stenocarpa** sp. nov.

Herbacea, caulibus gracilibus prope basem sparse pilosis; foliis vulgo rosulatis, spatulatis, pubescentibus; inflorescentia longa, laxe furcata; corollae hypocraterimorphae tubo saltem 2–plo calyce longiore, limbi lobis obtusis, plus minusve emarginatis; staminibus inclusis, 4 prope orificium tubi affixis, quinto circa medium tubi affixo, anthera sua circa 4 mm. antheris ceteris supposita; capsulis gracillimis, nondum dehiscentibus elongato-fusiformibus.

To at least 43 cm., more or less villose pubescent at base, retaining (short) pubescence on leaves, pedicel, calyx, corolla (aciculate and some little developed discoid-headed, on calyx few spheric-headed also, on corolla only aciculate and subaciculate hairs). Root slender tap (later?). Stems to 4 mm. diam. near base, erect or nearly so, simple or distantly forking. Leaves few, rosulate more or less spatulate, 9.5 × 2.5 cm., cauline smaller, narrower, shorter-petiolate. Inflorescence long, axis commonly forked or at least diverted by few, oblique-erect branches and pedicels, pedicels 4–8 mm., later 10–15 mm. Calyx slender, cylindric-campanulate, ca. 10 mm. long, tube conspicuously striped by dark midribs and intersepal membranes, teeth ca. ½ as long as tube, narrow, tapered, subequal. Corolla whitish in sicco, subsalverform, tube at least 20 mm. long (and probably longer?), ca. 2 mm. wide, a little dilated near mouth, inside ribbed below stamen insertions, limb shallowly, obtusely 5-lobed. Stamens included, 4 affixed near mouth of corolla tube, fifth affixed near middle, its anther several mm. (5–6 in type) lower than other anthers. Ovary slender-oblong, stigma barely exserted. Capsule equaling calyx, very slender fusiform, 12–13 mm. × ca. 2 mm., septicidal split not over ⅛ capsule length, loculicidal frequently shorter. Seeds ca. 0.8 mm. long, broadly oval-oblong, brown (Ridgway's hazel), honeycombed, ridges nearly straight, embryo bent.

Western Australia: Laverton, Sept., 1909, *Maiden*, TYPE (W).

Distinguishable from *N. suaveolens* by extremely slender capsule; from *N. rotundifolia* by stem glabrate above, flower longer, capsule longer and more slender.

12. **N. ingulba** Black, Trans. Roy. Soc. S. Austr., 57:156, pl. 9, fig. 1, 1933.

To 50 cm. or more, nearly glabrous (along leaf midrib occasional ephemeral aciculate or spheric-headed hairs; on pedicel, calyx, exterior of corolla, spheric- and discoid-headed). Root tap or soon terminating in laterals. Stems commonly several, ca. 2.5 mm. diam. near base, ascendent-erect, little branched. Rosulate leaves many, subpetiolate, narrowly spatulate or lanceolate, acute or acuminate, 10 × 3.5 cm., margin more or less undulate, cauline scarce, smaller, narrower, petiole short, frequently slightly winged. Inflorescence long, loose, sparingly branched, usually by forking; bracts sessile, slender, acute, soon reduced to 3–4 mm., pedicels 3–10 mm., later 8–15 mm. Flowers more or less erect. Calyx subcylindric, 12–17 mm. long, 10-ridged, scabridulous, teeth shorter than tube. Corolla tube 30–50 mm. long, 1.5–2.5 mm. wide, near mouth gradually, slightly dilated, limb ca. 25 mm. across. Four stamens affixed near mouth, fifth affixed near middle of corolla tube, its anther ca. 2 mm. below other anthers. Stigma barely exserted. Capsule narrowly elliptic, ca. 12 mm. long, shorter than or equaling calyx. Seeds 0.8–1.0 mm. long, compressed, or angular-subreniform, brown (Ridgway's cinnamon-brown), honeycombed, ridges nearly straight, embryo bent.

Central Australia: 1883, *Winnecke* (V); Harper's Spring, *Kramer*, TYPE (B?); between Finke River and Charlotte Waters, 1885, *Kempe* (V). Western Australia: Mount Squires, Aug. 28, 1891, *Helms* (V); Victoria Desert, Elder Expedition Camp 58,[10] *Helms* (V).

Distinguishable from *N. suaveolens* by very slender-tubed corolla, characteristically petiolate cauline leaves; from *N. Goodspeedii* by length and slenderness of corolla tube; from *N. megalosiphon* by scarcity and glabrousness of cauline leaves.

13. **N. rotundifolia** Lindley, Bot. Reg. Misc., 59, 1838.

N. fastigiata Nees, *in* Lehm., Pl. Preiss., 1:343, 1844.

N. suaveolens var. *rosulata* Moore, Jour. Linn. Soc., 34:206, 1898 (*N. rosulata* Domin, Biblioth. Bot., 22:592, pl. 36, fig. 11, 1929).

N. suaveolens var. *rotundifolia* Comes, Monogr. Nicot., 42, 1899.

Few cm. to 11 dm., distinct, patent, glistening hairs throughout, on younger portions very conspicuous (on inside of corolla, aciculate type; on outside, spheric-headed; elsewhere predominantly or exclusively spheric- and discoid-headed, former with lower cells often swollen and occasionally forming blunt villi as distal portion wears off). Root slender tap or somewhat irregularly branched near top. Stems 1–8, to 7 mm. diam. near base, slender above, erect, branched, sometimes forked, commonly purplish green, distinctly brittle. Leaves a little fleshy, undulate or plane, margin often repand, apex obtuse to barely acute or slightly mucronate, main lateral veins fairly distinct, rosulate leaves few, broadly spatulate, to rotund-, sometimes oblong-bladed and subpetiolate, to 20 x 6 cm., cauline sparse, smaller, broadly spatulate-obovate to elliptic-ovate with well-defined winged petiole, sometimes slightly auriculate, ultimately subsessile, oblanceolate to lanceolate. Inflorescence long, erect, branches more or less erect, numerous, usually alternate, short, bracts soon reduced to 5 mm. or less, sessile, acute, more or less appressed, pedicels 3–5 mm., later 8–20 mm. Flowers suberect to nearly horizontal, vespertine. Calyx greenish or purplish, more or less tubular, 6–8 or even 10 mm. long, membranes conspicuous, teeth about as long as tube, linear, subequal. Corolla tube 13–19 mm. long, 1.5–2 mm. wide, slightly but distinctly swollen below mouth, limb 8–10 mm. across, lobes obcordate. Four stamens affixed near mouth of corolla tube, fifth affixed in lower half of tube, its anther ca. 3 mm. below other anthers, anthers pale cream to purplish. Stigma commonly at or slightly below mouth. Capsule narrowly elliptic, usually 7–8 mm. long, about equaling calyx, septicidal scission nearly to middle, loculicidal often less. Seeds 0.7–0.8 mm. long, angular-oval, sometimes slightly subreniform, brown (Ridgway's hazel), rather faintly honeycombed, ridges minutely wavy, embryo bent. Chromosome number 22 pairs.

Southern Western Australia: Swan River, Jan., 1840, *Preiss* 1911, TYPE of *N. fastigiata* Nees (V); Hines Hill, Oct. 2, 1923, *Koch* (W); Kellerberrin, Dec., 1903, *Vachell* (W); Wilson's Pool, West Australian Goldfields, April, 1895, *Moore*, TYPE of *N. rosulata* (Moore) Domin (K); near Israelite Bay, Dec., 1884, *Brooke* (V); Elder Expedition Camp 61,[11] *Helms*, Sept. 25, 1891 (V).

Distinguishable from *N. suaveolens* by rotundly expanded cauline leaves, persistent glistening indument, smaller flowers. Lindley described the species from plants cultivated from seed received from R. Mangles, Sunning Hill, Swan River Colony, W. A.

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[10] 30° 14′ 5″ S, 123° 41′ 0″ E, 750 ft., Sept. 21, 1891 (cf. Trans. Roy. Soc. S. Austr., 16: 134, 1892–96).

[11] 30° 25′ S, 123° 8′ E, Victoria Desert (cf. Trans. Roy. Soc. S. Austr., 16: 130, 1892–96).

A scant-rooted obligate annual, rapidly maturing, setting seeds abundantly, soon dying unless pruned. Cleistogamy typical of cultures from Univ. Calif. Bot. Gard. accession 1927–1 (seed collected near Lake Grace, *Gardner*), chasmogonous flowers comparatively few, their occurrence influenced by conditions both internal and external to plant. Stigma usually slightly above anthers in chasmogonous flowers and no pollen germination within anther; in cleistogamous, stigma at anther level, receiving pollen tubes which pass through the slightly opened suture of the anther sac, dehiscence of anther incomplete. Both types of flower well formed, though development of cleistogamous arrested in early or later bud stages.

14. **N. Goodspeedii**[12] sp. nov.

Herbacea, caulibus gracilibus, erectis, glabris; foliis inferne numerosioribus, glabris, cauliniis oblanceolatis; inflorescentia longa, ramis plus minusve numerosis; floribus parvis, vespertinis, fragrantibus, corollae hypocraterimorphae tubo 2–3-plo calyce longiore, limbi lobis obtusis, emarginatis; staminibus in tubo corollae inclusis, 4 prope orificium tubi affixis, quinto infra medium tubi affixo, anthera sua circa 2 mm. antheris ceteris supposita.

1–11 dm., glabrous or nearly so in stem and leaf, inconspicuously puberulent elsewhere (bracts, pedicel, and calyx with spheric- and discoid-headed hairs, corolla with aciculate and spheric-headed outside, aciculate within lower part of tube). Root slender tap or divided near top into laterals. Stems 4–8, slender (3–6 mm. diam. near base), erect, forking. Leaves rather fleshy, margin plane or repand, apex usually acute, main lateral veins sometimes obscure on upper surface, rosette leaves numerous, oblanceolate or spatulate, to 24–32 × 5–7 cm., cauline leaves slender oblanceolate, few in weak or young plants, in best-developed merged below with rosette into cushion or "bunchy" base, above small, sparse. Inflorescence long, erect, more or less paniculiform, sometimes clearly forking, branches usually becoming erect, bracts soon reduced from linear oblanceolate to shortly ovate-lanceolate, ultimately ca. 3 mm. long, pedicels 4–9 mm., later 7–15 mm., buds on young inflorescences massed. Fowers directed obliquely upward, horizontal or nodding, vespertine, fragrance at night like strong honey (as *N. suaveolens*). Calyx tubular-campanulate, 6–8 mm. long, more or less distinctly 5-ridged by midribs, 5-striped by narrow intersepal membranes, teeth equal or subequal, sublinear, shorter than tube. Corolla salverform, tube 12–17 mm. long, 2–2.5 mm. wide, slightly inflated immediately below mouth, greenish, sometimes purplish outside, inside ribbed below stamen insertions, limb 6–11 mm. across, convolute plicate in bud, loosely so during day or on fading, otherwise spreading horizontally, white within, outside green-, cream-, or purple-tinged and green- or purple-nerved, sinuses very distinct, lobes subequal, obtuse, emarginate, sulcate. Stamens included, 4 affixed near mouth of corolla tube, fifth affixed in lower half, subarcuate-erect, its anther 2–3 mm. lower than other anthers, filaments pale greenish, anthers subrotund, yellowish or purple-tinged. Disc orange. Ovary oblong-ovoid, pale green, style nearly white, stigma green, subdiscoid, sulcate, generally at mouth, ca. 1 mm. above anthers. Capsule elliptic-oblong, 7–9 mm. long, subequal to or exceeding calyx, septicidal scission to middle, loculicidal less. Seeds compressed reniform, 0.56–0.75 mm. long, brown (Ridgway's chestnut), rugose, rarely areas where shallow depressions distinct, these subrhomboid, ridges a little wavy, embryo bent. Chromosome number 20 pairs.

Western Australia: Eucla, 1882, *Oliver* (V). South Australia: Ooldea, Sept. 24, 1920 (B); Fowler's Bay, 1879, *Richards*, TYPE (V); near Overland Corner, 1924 (B). New South Wales: Ivanhoe District, April, 1915, *Reuss* (W).

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[12] T. H. Goodspeed, Prof. Botany, Director Univ. Calif. Bot. Gard., engaged in the study of intrageneric relationships in *Nicotiana* for a number of years.

Distinguishable from *N. suaveolens* by tiny flower with corolla tube length characteristically 2.5 times as long as calyx; from *N. rotundifolia* by glabrous stem and leaves.

Cultures from Univ. Calif. Bot. Gard. accession 1927–13, 1932–18, 1932–19 (seed collected at Koonamore Station, S. A., *Osborn*) were remarkably similar to 1931–88 (seed collected at Forrest, southern Western Australia, *Baird*), although former segregated for size of plant, length of leaves. Garden plants regularly bloom before they are large enough to transplant from the flats; capsules mature in abundance, and flowers frequently become depauperate; life span brief unless prolonged by pruning.

15. **N. exigua** sp. nov.

Herbacea, caulibus assurgentibus, gracillimis, puberulentis aut glabriusculis, foliis cauliniis subpetiolatis, laminis ovatis, elliptico-ovatis, aut lanceolato-ovatis, superficiebus inferis plus minusve puberulentis, costis mediis superficierum utrarumque pubescentibus, vulgo hispidis; inflorescentia diffusa, floribus parvis, vespertinis; corollae hypocraterimorphae tubo 2–2.5-plo calyce longiore, limbi lobis subrotundis, emarginatis; staminibus inclusis, 4 prope orificium affixis, quinto prope medium tubi affixo, anthera sua circa 2 mm. antheris ceteris supposita.

To 5 dm. high, puberulent or subglabrate, becoming hispid along leaf midribs, commonly sparsely, minutely scabridulous on leaf surface or even stem (discoid-headed hairs from base of plant through calyx; aciculate not replaced by spheric-headed until inflorescence branchlets, reappearing inside lower part of corolla tube and on exterior of tube, on latter becoming spheric-headed near limb; modified spheric-headed with head two-celled common on pedicels, calyx). Root soon divided into laterals. Stems 1–6, to ca. 5 mm. diam. near base, soon very slender, assurgent, branching or forking, sometimes deep blue-purplish toward base and in inflorescence branchlets. Leaves rather thin, slightly fleshy, to 18 × 6.5 cm., blade passing obliquely into, then decurrent on quite well-defined petiole, margin undulate-erose, main lateral and usually lesser veins distinct, basal leaves rosulate at first, transition to lower cauline later less perceptible, blade elliptic-acute, that of cauline elliptic, ovate, or occasionally in upper ones broadly lanceolate, subacuminate. Inflorescence long, spreading, repeatedly branched, appearing more or less forked or jointed by smaller branches and pedicels, bracts linear-lanceolate or subulate, soon reduced to 2 mm., pedicels 3–9 mm., later 11–20 mm. Flowers directed obliquely upward or subhorizontal, vespertine. Calyx tubular or narrowly campanulate, 5–6 mm. long, frequently purple-nerved, intersepal membranes variable, often inconspicuous, teeth somewhat unequal, slender, shorter than tube, often tinged with purple, corolla salverform, tube 13–17 mm. long, ca. 2 mm. wide, slightly narrower within calyx, faintly swollen immediately below mouth, somewhat contracted at mouth, pale greenish cream or more or less purplish outside, inside pale greenish, ribbed below stamen insertions, limb 6–8 mm. across, convolute-plicate in bud, loosely so during day, otherwise spreading, lobes subequal, obtuse, emarginate, sulcate, white within, cream-, green-, or purple-tinged and green- or purple-nerved without. Stamens included, 4 affixed near mouth of corolla tube, fifth affixed near middle, its anther ca. 2–3 mm. below other 4 anthers, filaments pale greenish white, anthers subrotund, yellowish. Disc orange. Ovary conic-ovate, light green, style pale green, stigma thick-discoid or obconic, sulcate, barely exceeding anthers. Capsule conic-ovate to even subpyriform-ovate, 6–8 mm. long, subequal to or exceeding calyx, septicidal scission to about middle, loculicidal less or sometimes lacking. Seeds subreniform, ca. 0.7 mm. long, brown (Ridgway's hazel), rugose, ridges wavy, embryo bent. Chromosome number 16 pairs.

Queensland: Univ. Calif. Herbarium 519503, Univ. Calif. Bot. Gard. plant, 31424 P6, grown from garden accession 1931–59, namely, seed from Dalby, Queensland, *McCarthy*, TYPE (UC).

Distinguishable from *N. suaveolens* by tiny flower. Intermediate between *N. Debneyi* and *N. Goodspeedii;* distinguishable from former by lack of leaf auricle, high stamen insertion, from latter by broader, distinctly veined leaves, spreading habit, pubescence.

DOUBTFUL OR INSUFFICIENTLY KNOWN

N. anisandra Vest, Flora, 4:147, 1821 = ?

"Caule herbaceo tereti glabro, foliis sessilibus oblongis basi angustatis undatis glabris, corollae tubo cylindrico duplo calycis scabri longitudine, limbi laciniis rotundatis, calycinis sublatis, anthera unica longius pedicellata tribus in fauce sessilibus... Corollae lutescentes, tubo longo, sesquipollicari... Antherae tres subsessiles in fauce, quarta filamento ultra medium elata, quinta supra medium tubi subsessilis... A *N. suaveolente* differt: Filamentis quatuor longitudine tubi et foliis subpetiolatis... Habitat—?"—Vest.

Description detailed, but long calyx, difficulty in interpreting length and insertion of stamens from statements quoted above, and lack of any record of locality makes identification without specimen uncertain. Note, however, that stamen characters, although rather constant, are not rigidly fixed in a species, lowest anther sometimes is subsessile in upper half of corolla tube in tetraploid *N. suaveolens,* and relative length and point of insertion of four longer stamens is a little unequal and variable in several species. Comes's suggestion of *N. suaveolens* Lehm. possible.

N. australis R. Br. ex Comes, Monogr. Nicot., 41, 1899 = nomen nudum?

N. Forsteri Roem. and Schult., Syst., 4:323, 1819 = ?

Species based on New Caledonian plan which Forster had referred with some doubt to *N. fruticosa* L. Some evidence, now being checked, that type specimen may = *N. Debneyi* Domin.

N. mirabiliflora Dietr. ex Comes, Monogr. Nicot., 39, 1899 = nomen nudum?

N. Neesii Lehm., Pl. Preiss., 1:344, 1884 = *N. rotundifolia* Lindl.?

Near Mount Brown, York, Western Australia, *Preiss* 1912, TYPE. Description fits small, young plant of *N. fastigiata* Nees save for slightly larger flowers, although Comes places *N. Neesii* under *Nierembergia.*

N. obtusisepala Domin, Biblioth. Bot., 22:594, 1929 = *Petunia* sp.?

Hughenden, Queensland, Feb., 1910, *Domin,* TYPE. Type not examined, but long-pediceled, axillary-appearing flowers, corolla limb lobes more or less acute, and calyx parted are characters of *Petunia axillaris* (Lam.) B. S. P.

"Ich hielt diese Art [*N. obtusisepala*] zunächst für eingeschleppt, da sie in der allernächsten Umgebung von Hughenden und sogar im Städtchen selbst als Unkraut wuchs... Die Einfugung der Antheren entspricht auch dem *suaveolens*-Typus."—Domin.

N. suaveolens

var. **anisandra** (Vest) Comes, Monogr. Nicot., 42, 1899, cf. *N. anisandra* Vest

var **Debneyi** Bailey, Queensl. Fl., 4:1096, 1901 (cf. also Bailey, Compreh. Cat., fig. 335, 1913) = ?

"Monkira Station, Diamantina River, South West Q'ld," Aug., 1891, *Debney,* TYPE (Q). Type has calyx 13 mm. long, corolla tube 25 mm. long, 4.5 mm. wide, limb 18 mm. (or more) across, and apparently no ellipsoid-headed hairs. Suggests small-flowered *N.*

suaveolens Lehm. rather than *N. Debneyi* Domin, but more extensive material desirable for determination.

var. **parviflora** Benth., Fl. Austr., 4:470, 1869 = at least *N. Debneyi* Domin, possibly *N. exigua* Wheeler, *N. Goodspeedii* Wheeler, *N. velutina* Wheeler

Queensland, north New South Wales. "Corolla much under 1 in. long. Leaf-petioles sometimes auriculate, sometimes not. Panicle large and loose."—Bentham.

var. **tuberosa** Comes, Monogr. Nicot., 41, 1899 = *N. fragrans* Hook.?

New Caledonia. Comes cites *Viellard* in hb. New Caledonia, *Lenormand* in hb. Cand., and describes the variety as "caule basi incrassato, tuberiforme; fol. imis lanceolatis spathulatisve, subintegris, acutiusculis; tubo corollino longissimo."

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INDEX TO AUSTRALASIAN SPECIES OF NICOTIANA

(Synonyms in *italics;* new species in **boldface.**)

PAGE

- anisandra 65
- *Australasiae* 58, 59
- australis 65
- Benthamiana 49
- Debneyi 51
- excelsior 50
- **exigua** 64
- *fastigiata* 62
- fragrans 52
- Forsteri 65
- **Goodspeedii** 63
- Gossei 53
- ingulba 61
- *Macgillivrayi* 52
- *macrocalyx* 50
- **maritima** 56
- megalosiphon 54
- mirabiliflora 65
- Neesii 65
- obtusisepala 65
- **occidentalis** 52
- *rosulata* 62
- rotundifolia 62
- **stenocarpa** 61
- suaveolens 57
  - var. anisandra 65
    - *cordifolia* 49
    - Debneyi 51, 65
    - *excelsior* 50
    - *longiflora* 54
    - *macrantha* 52
    - *parviflora* 51, 66
    - *rosulata* 62
    - *rotundifolia* 62
    - tuberosa 66
    - *undulata* 58, 59
    - *vincaeflora* 58, 59
- *undulata* 57, 58
- *vincaeflora* 58, 59
- **velutina** 55

A SYSTEMATIC STUDY OF THE GENUS ERIOPHYLLUM LAG.

BY

LINCOLN CONSTANCE

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CONTENTS

PAGE

Historical introduction 69

Relationships with allied genera 71

Phyletic tendencies within the genus 72

Geographical distribution 74

Geological record 78

Acknowledgments 78

Taxonomic treatment 79

Species excluded 121

Literature cited 122

Explanation of plates 123

A SYSTEMATIC STUDY OF THE GENUS ERIOPHYLLUM LAG.

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HISTORICAL INTRODUCTION

THE GENUS *Eriophyllum* was published by Lagasca (1816) with two species, *E. trollifolium* and *E. staechadifolium,* based upon material obtained by the Malaspina Expedition. The first two species were both perennial, and, although *E. trollifolium* has priority of place, *E. staechadifolium* should be interpreted as the type species since it has been satisfactorily identified while *E. trollifolium* has not. The validity of the generic name was a matter of some doubt until 1883, because the location of "Real del Monte" (site of the original collections) was mistakenly attributed to Mexico instead of to California, the type collections were early lost, and certain discrepancies in the original diagnoses were revealed. With the establishment of the type locality, however, and the determination of the type species, *Eriophyllum* Lag. has now become generally accepted.

Pursh (1814) described specimens collected by Lewis (in what is now northwestern Idaho) as *Actinella lanata,* but, in the author's opinion, referred them to the wrong genus. Doubtless unaware of Lagasca's earlier paper, Nuttall (1818) published the new genus *Trichophyllum,* based upon *Actinella lanata* Pursh. Sprengel (1825), who minimized generic distinctions, placed both *Eriophyllum* and *Trichophyllum* under *Helenium* L. An illustration and written description of *Eriophyllum caespitosum* Douglas (1828), the second use of the original generic name, appeared in Lindley's Botanical Register for 1828. Sprengel (1831) placed together *Eriophyllum caespitosum* Douglas and *Trichophyllum lanatum* (Pursh) Nutt., and erected upon this combination the nebulous genus *Phialis.* He attempted to distinguish *Phialis* from *Eriophyllum* by attributing to *Phialis* a gamophyllous involucre, yet stating that the structure was polyphyllous in *Eriophyllum,* although this character is variable and a completely united involucre unknown. De Candolle (1836) placed all the foregoing species under *Bahia* Lag., believing Lagasca's two genera to be insufficiently distinct. In addition, he erected a new genus, *Actinolepis,* based upon the annual, *A. multicaulis* DC. Except for the publication of subsequent new species, no improvement was made upon this arrangement for nearly half a century.

Asa Gray (1876, 1884) was the first who undertook to give the synonymy, geographical distribution, and some clue to the natural relationships of the present genus *Eriophyllum* and its species. He (1883) critically appraised the generic distinctions which had been used to characterize *Bahia* Lag., *Erio-*

phyllum Lag., *Actinolepis* DC., and allied genera. All perennial species with involucral bracts permanently erect and carinate, and pappus paleae unthickened at base, were placed in *Eriophyllum,* and there constituted the section *Trichophyllum* (Nutt.). Gray judged *Actinolepis* to be not generically distinct from *Eriophyllum,* and used it to form a second section, embracing the greater part of the annuals. The first critical treatment of the genus in anything approaching entirety appeared in the Synoptical Flora (1884, 1886), wherein Gray attempted to place in their proper circle of affinity all the previously named species, many of which he reduced to varietal rank or degraded to synonymy. In this flora (the final expression of his ideas in regard to the group), he recognized a total of twelve species and seven varieties.

Since 1890, the published species of *Eriophyllum* have been multiplied until, at the present time (including specific, varietal, and herbarium names), there are approximately 157 designations for members of the genus. The only attempt at a complete treatment of the genus since Gray's is that of Rydberg (1915), in the North American Flora. Here, sixteen new species are described, seven names which had fallen into synonymy are resurrected, and three genera are segregated from the genus (as it appeared in the Synoptical Flora). The genus *Eriophyllum* is credited with forty-five species; *Actinolepis,* with two; and *Antheropeas,* a new segregation of annual species, with five, making a total of fifty-two species and no varieties.

Since the time of Gray's treatment in the Botany of the California Geological Survey, the genus has (in California) received the successive attention, notably, of Greene, of Hall, and of Jepson. Greene (1897) preceded Rydberg in reëlevating *Actinolepis* DC. to generic rank, and described a number of new segregates, recognizing (in all) some twenty-one species and two varieties of these two genera in California and adjoining areas. Hall (1907) gave critical attention particularly to the annual species, reducing a number of described forms to synonymy. Jepson (1925) has followed the same procedure in regard to the perennials, allowing only thirteen species and thirteen varieties for the State.

Recent floras and all herbaria examined show a strong diversity of treatment: some systematists adhere to the conservative treatment of Gray; others accept the segregates of Greene, Rydberg, and others; and a third group vainly attempts to bring the two schools into working harmony. Because of these different attitudes, few herbaria are uniformly or consistently labeled, and the student attempting to determine specimens is almost sure to be baffled by the resulting confused nomenclature.

It was the recognition of this disorder which inspired the present reëxamination of the genus, utilizing modern lines of investigation. The writer has attempted to explain some of the perplexing variation exhibited within the genus by correlating it with facts of ecology and geographical distribution, observed in garden and field; to make intelligible the involved synonymy by careful examination of the type specimens of doubtful species and through exhaustive investigation of the literature; to identify the numerous artificial segregates, and to restore them to their proper position in the genetic scheme; to delimit, so far as possible, natural specific and varietal populations; and to construct a key which will allow for the wide play of natural variation.

In this paper, the term *species* is used to designate any natural population of morphologically similar, genetically interfertile individuals, isolated in one manner or another from all other such populations. Only four or five of the several thousand specimens examined appear to cross this barrier. Populations possessing certain morphological features in common and occupying a coherent geographical range, but closely connected with adjoining populations by intermediate forms, will be considered *varieties*. The only subunits which have been admitted fulfill the requirements of *subspecies*, in the usage of Du Rietz (1930), but the traditional term *variety* has been retained to avoid the necessity of making further new combinations. Minor variants of sporadic occurrence are discussed but are not given separate nomenclature.

RELATIONSHIPS WITH ALLIED GENERA

Eriophyllum is placed in the tribe Helenieae (Compositae) because of the 1-seriate involucre, the commonly naked receptacle, the noncaudate antherbases, and the paleaceous pappus. In the Genera Plantarum of Bentham and Hooker (1873), the genus (treated together with *Bahia* Lag.) is assigned to the subtribe Baerieae (of Helenoideae) by reason of its 1-seriate, subequal involucral bracts, pistillate rays, and narrow, angled achenes. Gray (1884) combined the subtribes Euhelenieae and Baerieae (of the Genera Plantarum) into the subtribe Helenieae, including *Eriophyllum* here because of its deciduous rays, in addition to the characters already mentioned. Hoffmann (1894) followed Gray, with some minor modifications. The tribe Helenieae is broken up into no less than fourteen subtribes by Rydberg (1915), nine more than distinguished by Bentham and Hooker, and ten more than admitted by Gray and by Hoffmann. In Rydberg's treatment, *Eriophyllum* (in spite of its perennial species) is included in subtribe Eriophyllanae, with *Monolopia* DC., *Syntrichopappus* Gray, and other exclusively annual genera. The closely related Bahia becomes the type genus of another subtribe, Bahianae. These divisions are so obviously artificial that the writer disregards them in favor of the usage of Gray and of Hoffmann.

In the view of the author, and with reference to certain earlier treatments, the present genus may be set apart from related groups with which it has been confused, as follows: *Eriophyllum* is distinguished from *Bahia* Lag. and *Helenium* L. (to which certain of the perennials have previously been referred) by its characteristically woolly herbage and permanently erect, carinate involucral bracts; from *Monolopia* DC. section *Pseudobahia*, by the unflattened achenes, usually free involucral bracts, and presence of pappus (Constance, 1934), although this last relationship is very close; and from *Eremonanus* Johnston, by the naked (rarely somewhat paleaceous or scrobiculate) receptacle.

The perennial species of *Eriophyllum*, which are probably of more ancient origin than its annuals, relate it to certain perennial species of *Bahia,* the geographical distribution and morphological characters of which suggest an affinity between the two genera.

PHYLETIC TENDENCIES WITHIN THE GENUS

Most synantherologists have not hesitated to affirm that two paramount tendencies are operative in the inflorescence of the Compositae: (*a*) reduction, or economy, and (*b*) aggregation and condensation. By following the course of these two evolutionary trends and applying certain of the Besseyan criteria, even the amateur in phyletic speculation is enabled to trace a few apparent relationships within the present group.

So far as the genus *Eriophyllum* is concerned, the following characters are indicated as probably primitive:

(*a*) perennial habit, as opposed to annual habit;
(*b*) solitary or few, large, long-peduncled heads, as opposed to numerous, smaller, short-peduncled or sessile heads;
(*c*) hemispheric involucres, with rather numerous bracts, as opposed to narrower ones, with fewer bracts;
(*d*) heads radiate, the rays large and rather numerous, as opposed to discoid heads (radiate heads with few, inconspicuous rays being intermediate);
(*e*) pappose, as opposed to epappose, achenes;
(*f*) yellow ligules, as opposed to those of other colors.

Characters of foliage, pubescence, achene surface, and the like, are all too variable to be of much value in this connection, and most of the other structures are too stereotyped to be so employed.

The foregoing dicta would lead to the choice of the widespread and variable *Eriophyllum lanatum* as most nearly representing the primitive stock of the genus. Within the species, it is more difficult to choose which of the various subunits should be selected as basal. *E. lanatum* var. *achillaeoides* seems most closely related to the other perennial species, and its occurrence fits in with the suggested generic center of dispersal. It is significant, however, that *E. lanatum* var. *grandiflorum* occurs on Guadalupe Island (two hundred miles southwest of the southern boundary of Alta California), and as such gives evidence of having had a much more comprehensive range than it exhibits today. The Guadalupe Island plant is somewhat intermediate between the two varieties of *E. lanatum* just mentioned, and it is not improbable that a population ancestrally common to both was the true primitive stock.

The operation of the tendency to aggregation and to reduction is observable in the inflorescence of some members of *Eriophyllum lanatum* and in *E. Jepsonii* and culminates in the corymbiform inflorescence of the three other perennial species. *E. Nevinii* is obviously related to *E. staechadifolium* and was doubtless derived from that species incident upon isolation. The progression from *E. lanatum* to *E. confertiflorum,* by way of *E. Jepsonii,* is not difficult to trace, since the last is intermediate in a number of features.

The derivation of the annual species is far less easy to ascertain. It is presumed that *Eriophyllum nubigenum* and *E. ambiguum,* which agree in form of style-tips and anther-apices with the perennial species, connect these with the other annuals. *E. Wallacei* and *E. lanosum* are closely linked by their advances in ray color (sporadic in the first but nearly stabilized in the second) and by their peculiar subulate anther-tips. They are possibly derived from the same source as *E. ambiguum*. *E. Pringlei* is doubtless an eradiate descendant of the closely related *E. multicaule,* but the clustered, nearly sessile heads and boat-shaped bracts separate these two from all the other annuals and suggest *E. confertiflorum.* This resemblance is, perhaps, only a striking parallelism in development. *E. lanatum* var. *integrifolium* exhibits marked reduction in habit and in number and size of parts, as well as condensation and narrowing of leaves, so the origin of all but the last two of the annual species may, conceivably, be traceable to it.

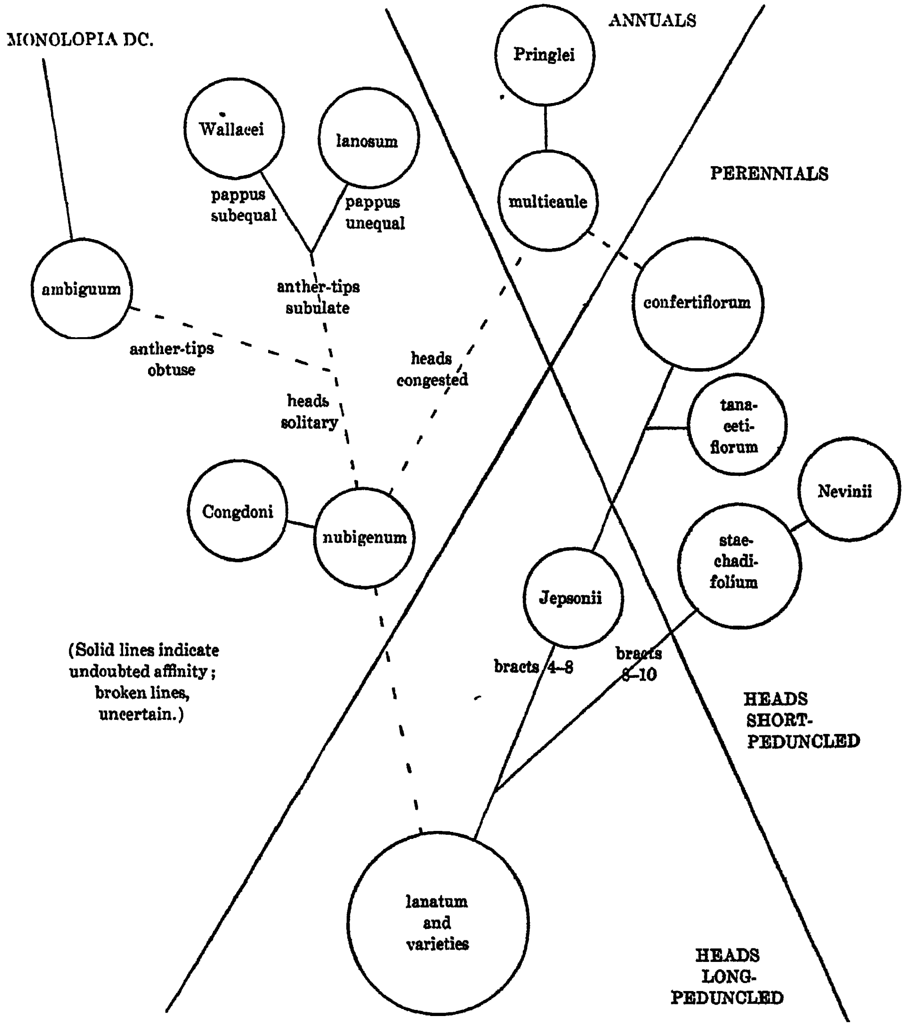

Fig. 1. Phyletic tendencies within the Genus.

GEOGRAPHICAL DISTRIBUTION

The geographical distribution is indicated by the accompanying maps (figs. 2, 3, and 4). In general, the annual species are confined to desert areas and adjoining ranges (Austral life zones), while the perennials occupy less xerophytic habitats (Boreal, Transition, and Upper Sonoran life zones). Altitudinal stratification is not well defined in the perennial species, although certain subunits of *Eriophyllum lanatum* are rather closely restricted to definite horizontal belts.

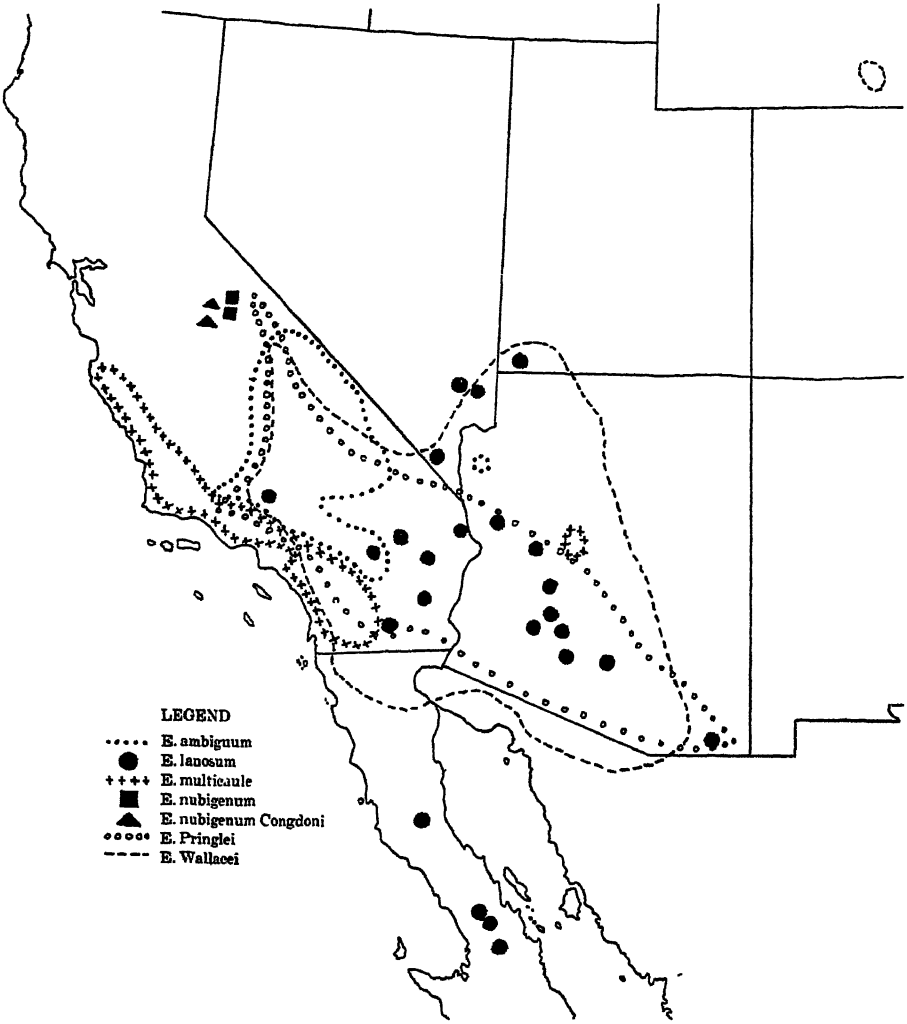

Fig. 2. Map showing distribution of Annual Species.

In the author's opinion, the center of dispersal of the genus was in the California Inner Coast Ranges, between San Francisco Bay and the junction of

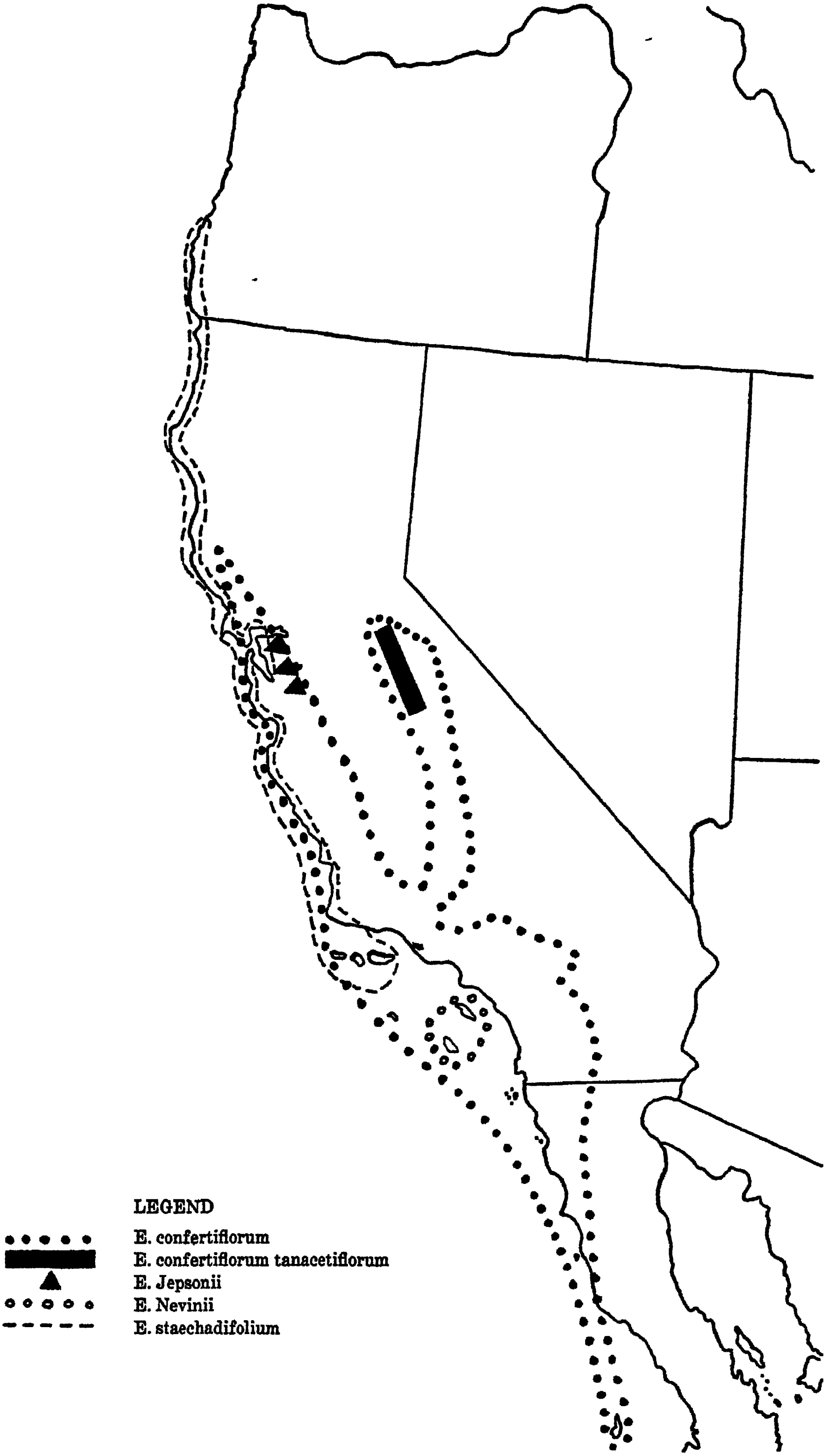

Fig. 3.—Map showing distribution of Perennial Species, exclusive of *E. lanatum.*

the Los Angeles Ranges* with the Sierra Nevada. Three of the perennials and *Eriophyllum multicaule,* of the annuals, are found here and the other two perennial species are not far distant. The annuals probably have had a more recent period of dissemination, from the western rim of the Sonoran desert (Mohave division).

The most interesting problems of migration are involved in the movements of the morphologically primitive *Eriophyllum lanatum.* The writer believes that the range of this species has undergone a marked shift northward from the center of dispersal. In southern California, it is represented by a few, nearly distinct varieties; in northern California, by a larger number of less well defined subunits; and in the Northwest, by a few widespread, more nearly homogeneous populations. The first indicates the action of "progressive reduction of variability" incident upon isolation, in an area where the present climate permits persistence but not active colonization. North of this region, various factors are promoting the differentiation of the species into regional varieties and local races, the isolation of which has not been completed and which are still attached to neighboring populations by connecting series. Conditions in the Northwest seem to favor rapid spread without marked differentiation, aside from the formation of the two varieties on the opposing sides of the Cascade divide.

It must be remarked that this movement might also be interpreted as having taken place in the reverse direction (from north to south). According to this view, the forms of southern California are persistent remnants of successive waves of migration from the north. The author would oppose this view on two counts: (*a*) There are no conceivable ancestral types of this genus in the Northwest, and these are represented in the Mexican region, to the south. (*b*) The center of dispersal of the tribe Helenieae is generally accepted to lie in this Mexican region, so paths of migration would be expected to lead *away from,* not *toward,* this area.

An alternate interpretation is that increasing aridity of the Californian climate has caused a progressive segregation of the originally homogeneous species, which retains its primitive character only in the Northwest. The writer is inclined to favor the first explanation, because of the appearance of tendencies in *Eriophyllum lanatum* var. *achillaeoides* that are further developed in derivative species, although this may be only parallelism of development (stimulated by action of similar environmental factors) rather than evidence of hereditary connection.

Finally, it should be mentioned that the occurrence of *Eriophyllum lanatum* on Guadalupe Island and, in the southern part of its range, on geologically positive areas generally, indicates a once more abundant distribution in the area in which it is now poorly represented. Number of individuals and general

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* Geographical names used in this paper are taken chiefly from Fenneman, Physiography of the Western United States (New York, McGraw-Hill, 1931). His nomenclature is too extensive to permit of its being summarized here, but should its use in any instance admit of possible misinterpretation, fuller explanation is made. For further information, the reader is referred to Fenneman's text and the accompanying map.

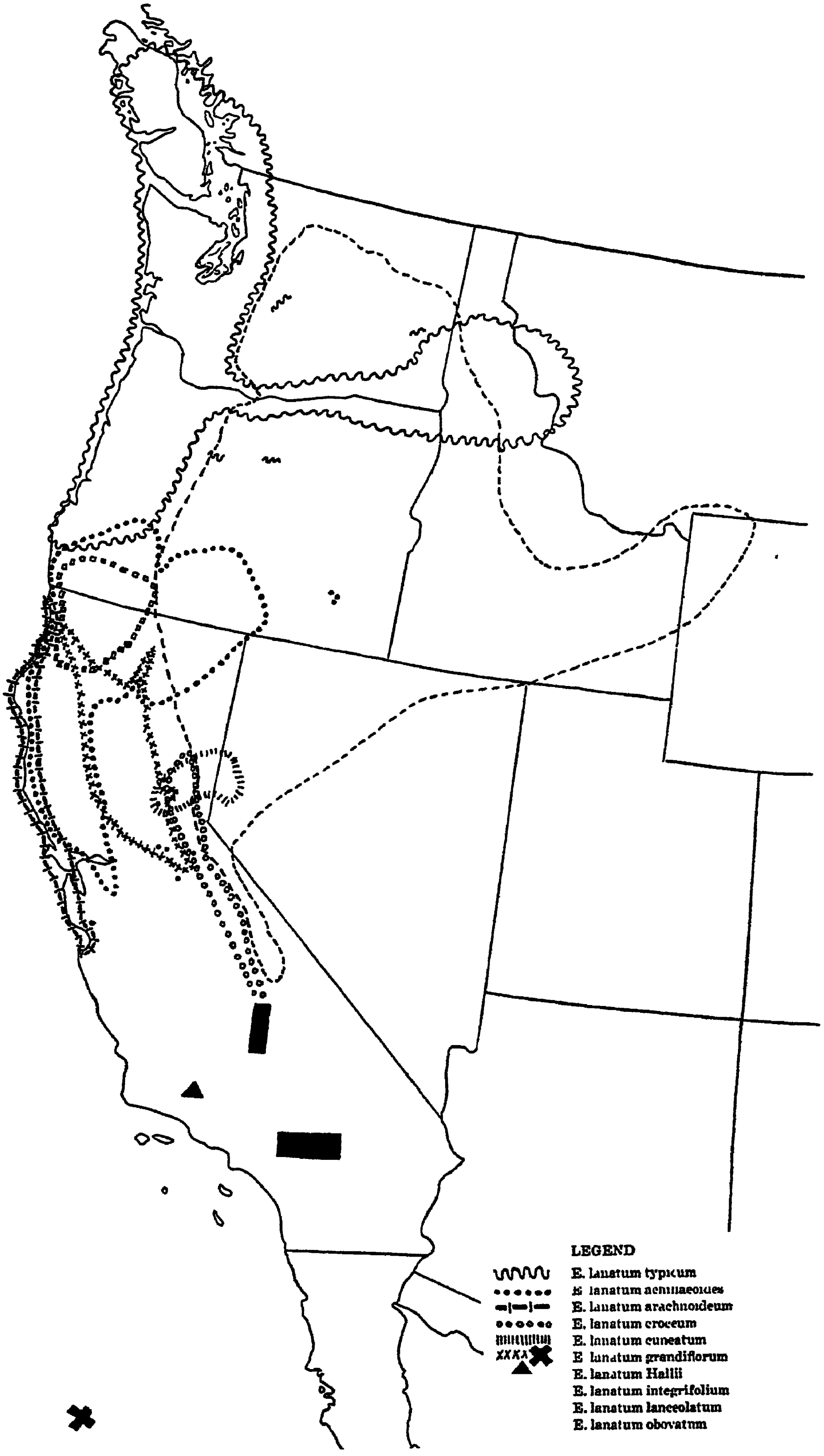

Fig. 4. Map showing distribution of *E. lanatum*.

instability of structure would point to the existence of two modern centers of dispersal for this species: one in the Klamath area, the other in the Sierra Nevada foothills (in the vicinity of Plumas and Nevada counties).

GEOLOGICAL RECORD

Mason (1934) reports a spatulate, pinnatifid fossil leaf, with recurved margins, from Pleistocene deposits at Tomales Bay (Marin County, California). He assigns the specimen to *Eriophyllum artemisiaefolium* O. Ktze. (a phase of *E. staechadifolium*), and the writer has confirmed this identification. This is the only published paleobotanical record of any member of the genus. The species still occupies this area, which would lead to the conclusion that conditions here have remained relatively stable and suitable for the persistence of this plant over a long period of time.

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ANSP	Academy of Natural Sciences, Philadelphia
BC	Provincial Museum of Natural History, Victoria, B. C.
CAN	National Museum of Canada, Ottawa
CAS	California Academy of Sciences, San Francisco
GENEVA	Conservatoire Botanique de la Ville de Genève
GRAY	Harvard University, Gray Herbarium
KEW	Royal Botanic Gardens
O	University of Oregon, Eugene
P	Pomona College, Claremont, California
R	Rancho Santa Ana Botanical Garden, Anaheim, California
RM	University of Wyoming, Rocky Mountain Herbarium, Laramie, Wyoming
S	Stanford University, Dudley Herbarium
UC	University of California
UCLA	University of California at Los Angeles
USNH	United States National Herbarium, Washington, D. C.
UW	University of Washington, Washington State Museum, Seattle
WSC	State College of Washington, Pullman, Washington
WU	Willamette University, Salem, Oregon

The writer is sincerely grateful, also, to Dr. Jepson for the use of a working collection of the flora of California, and to the following persons for the privilege of examining the specimens of this genus in their private herbaria: Miss Mary L. Bowerman, Berkeley; Mr. Victor Duran, Berkeley; Mr. Joseph A. Ewan, Los Angeles; Mrs. Jean Linsdale, Berkeley; Dr. Herbert L. Mason, Berkeley; Mr. Frank W. Peirson, Altadena.

A complete set of the author's collection of *Eriophyllum* has been deposited at the University of California, Berkeley, and partial sets at the California Academy of Sciences, University of Oregon, University of Wyoming, University of California at Los Angeles, and University of Washington.

In the following treatment, full citation is given of *critical* herbarium material only. Other citations, for reasons of economy, are given with the greatest possible brevity, simply to serve as verification for the ranges given on the maps (figs. 2, 3, and 4). Since biographic areas have not been generally and satisfactorily delimited, the arrangement by political units will enable botanists working with an atlas to obtain at least an approximate idea of the distribution of the various species.

TAXONOMIC TREATMENT

Eriophyllum Lagasca

Eriophyllum, Lagasca, Gen. et Sp., 28. 1816.
Trichophyllum, Nuttall, Gen., 2:166. 1818.
Helenium, Sprengel, Syst., 3:573 (in part). 1825—Not *Helenium* L., 1753.
Phialis, Sprengel, Linn. Gen. Pl., 631. 1831.
Actinolepis, De Candolle, Prodr., 5:655. 1836.
Bahia, De Candolle, *l. c.,* p. 656 (in part).—Not *Bahia* Lag., 1816.
Antheropeas, Rydberg, N. Am. Fl., 34:97. 1915.

ORIGINAL DESCRIPTION

"G. N. ERIOPHYLLUM. Ord. Nat. Corymbiferae. Juss. Char. gen. diff. Anthod. simplici serie 8–11-phyllum, multiflorum, erectum. Corolla radiata; radiis lingulatis, 8–11. Receptac. nudum, excavato-punctatum. Semina oblonga, tetragona, basi acuta. Pappus paleaceus, 4–8-phyllus." (Lagasca, 1816.)

AMPLIFIED DESCRIPTION

Suffrutescent plants, and perennial or annual herbs. Herbage tomentose or floccose, wool often partly deciduous. Leaves prevailingly alternate (mostly opposite on seedlings and young shoots), sometimes entire, but usually variously toothed, lobed, or divided. Involucres campanulate or hemispheric. Bracts 1-seriate (sometimes appearing 2-seriate); firm and permanently erect, becoming somewhat concave and embracing ray-achenes; distinct or slightly united at base. Receptacle convex to nearly flat, naked (occasionally with a few slender hyaline scales in one species), foveolate. Rays ligulate, 1-seriate, usually few (sometimes wanting), pistillate and fertile, without appendages. Disk-florets few to many, regular, hermaphrodite, mostly fertile; tube of disk-corollas glandular or hairy or both (except in one variety of *E. lanatum*), equaled or exceeded by campanulate or oblong throat. Anthers obtuse at base, apical appendages present. Pollen grains spherical, echinate. Style-tips blunt, rarely acute. Achenes slender, 4-angled, at least those of disk not flattened. Pappus of firm, nerveless, noncostate, hyaline or opaque paleae, usually erose or fimbriate, seldom obsolete.

Range.—Temperate western North America.

As stated above, Gray (1883) merged *Actinolepis* DC. and *Eriophyllum* Lag. under the latter name. He retained *Actinolepis* (DC.) and *Trichophyllum* (Nutt.) as distinct sections of *Eriophyllum.* The major distinction between the two sections, whatever may have been intended in the beginning, soon became chiefly that of annual as opposed to perennial habit. But Gray was unable to separate the annual *E. ambiguum* from the perennial section, so the distinction between the two was essentially meaningless.

Rydberg (1915) divided *Eriophyllum* into three proposed genera, but retained annual species in each of them: *Actinolepis, Antheropeas,* and *Eriophyllum.* It would be possible to keep the sections of Gray, and to make another of *Antheropeas.* In each division, however, the sectional segregations

KEY TO THE SPECIES OF ERIOPHYLLUM

A Perennials; plants suffruticose at least at base.
B Heads small (1.5 cm. or less in breadth), sessile or short-peduncled (3 cm. or less) in terminal clusters.
C Involucral bracts 8–12, oblong, little overlapping; rays 6–9.
D Leaves equally tomentose on both surfaces; ligules short, 2 mm. long, 1 mm. broad; San Clemente and Santa Catalina islands.............5. *E. Nevinii*
DD Leaves glabrate above, tomentose beneath; ligules 3–5 mm. long, 2–3 mm. broad; coastal, and northern Santa Barbara Islands...4. *E. staechadifolium*
CC Involucral bracts 4–7, ovate, strongly overlapping; rays 4–6 (often wanting).
E Involucres 5–7 mm. high, 5–6 mm. broad; disk-florets 3.5–4 mm. long; achenes about 3.5 mm. long.........3a. *E. confertiflorum tanacetiflorum*
EE Involucres mostly 3–5 mm. high, 3–5 mm. broad; disk-florets 2.3 mm. long; achenes 2–3 mm. long.....................3. *E. confertiflorum*
BB Heads large (1.5–3 cm. broad), long-peduncled (3 cm. or more), solitary or loosely corymbose.
F Plants shrubby throughout; narrowly endemic species, central California Coast Ranges................................2. *E. Jepsonii*
FF Plants shrubby only at base; wide species.............1. *E. lanatum*
AA Annuals; plants herbaceous throughout.
G Heads solitary on naked peduncles; receptacle conspicuously conical or convex.
H Anther-appendages ovate or lanceolate.
I Pappus 0.5–2 mm. long; middle Sierra Nevada.
J Rays inconspicuous, 4–6; peduncles 0.5–1.5 mm. long.... 6. *E. nubigenum*
JJ Rays conspicuous, 8–10; peduncles 3–10 mm........... 6a. *E. nubigenum Congdoni*
II Pappus less than 0.5 mm. long or obsolete; desert area of southern California and bordering ranges...7. *E. ambiguum*
HH Anther-appendages linear-subulate.
K Pappus of unequal hyaline paleae, the alternate awnlike, the others obtuse................8. *E. lanosum*
KK Pappus of subequal obtuse opaque paleae, or reduced to a short crown....................9. *E. Wallacei*
GG Heads sessile in leafy-bracteate terminal clusters; receptacle nearly flat.
L Heads radiate; tomentum of cauline leaves deciduous.........................10. *E. multicaule*
LL Heads discoid; tomentum persistent........... 11. *E. Pringlei*

would rest upon only one or two characters; *Actinolepis* and *Antheropeas* would (in the opinion of the writer) contain but two species each, and *Trichophyllum* would remain with two annual species in addition to all the perennials. In short, the annual species would simply be more unnaturally dispersed than ever.

In recognizing only eleven species and twelve varieties, I believe it unnecessary to retain any of the divisions mentioned. The genus may be handled in its entirety with relative ease (as here constituted), and the sectional differentiation would imply a disunity which, to my mind, does not exist. The transition from the perennial to the annual habit is shown in the occasional occurrence of the latter in *Eriophyllum lanatum* var. *achillaeoides* (*E. idoneum* Jepson), so even this distinction need not be considered peculiarly decisive.

1. Eriophyllum lanatum (Pursh) Forbes

Eriophyllum lanatum (Pursh) Forbes, Hort. Woburn., 183. 1833.

Perennial, with conspicuous tomentum, persistent or partly deciduous in age. Herbaceous stems few to numerous, erect or ascending, branching or simple, mostly 1–10 dm. high, from decumbent, suffruticose base. Leaves variable, narrow or broad, usually more or less toothed or divided, 1–8 cm. long, not subcoriaceous. Heads large (1–3 cm. broad with expanded rays), long-peduncled, terminal, solitary to many, then loosely corymbose. Peduncles 3–30 cm. long. Involucres campanulate to hemispheric, tomentose or floccose (at least in youth), 6–10 mm. high, 6–15 mm. broad. Bracts 5–15, lanceolate to ovate, acute or obtuse, carinate, more or less overlapping but distinct (or slightly united at base.) Receptacle convex (nearly flat to subconic), foveolate. Rays usually same number as bracts (not rarely wanting), oblong or oval ligules yellow, notched or toothed at apex. Disk-florets numerous (20–150), throat narrowly campanulate or oblong, usually exceeding short tube, which (except var. *Hallii*) is more or less glandular or glandular-hairy. Anther-appendages triangular-ovate, obtuse. Style-tips subcapitate, truncate, or obtuse. Achenes 2.5–4 mm. long, 4-angled, tapering to base, and variously hairy, glandular, or bald. Pappus of 6–12 hyaline scales, of diverse shape and length, usually erose or lacerate, sometimes reduced to a toothed crown, or completely obsolete.

Range and synonymy are given under the discussions of the various subunits.

Of the 157 binomials and trinomials which have been applied to members of *Eriophyllum,* 75 are referable to this one species! Granted that it is a huge and polymorphous entity as retained by the writer, it has been enlarged to include only three more groups than were assigned to it (under *E. caespitosum*) in the Synoptical Flora. Gray (1876) wrote of this, "It seems impossible to distinguish the forms here indicated into species." The writer directed his attention particularly to this species, and reached a similar conclusion after extensive field work, garden study, and the careful analysis of hundreds of herbarium specimens. The most difficult task connected with the whole problem has been the attempt to ascertain the affinities of the numerous artificial segregates, and to place them in their proper relation to the species-population.

The whole population were, perhaps, better treated as a single polymorphous (actively differentiating?), extremely plastic species. The extreme forms, however, are so strikingly dissimilar, and the differences of the wide habitat are so great, reflecting themselves in the local vegetative forms, that such a treatment would scarcely meet with general acceptance. Accordingly, it is attempted to distinguish within this species certain recognizable aggregations showing some constancy in certain combinations of characters, and geographically coherent. Some of these appear distinct enough to be species, and perhaps some are, although the writer has been unable to convince himself upon that point. Others appear well defined in the central portion of their range, but so intergrade on their borders with adjacent races that it is practicable to delimit them arbitrarily. Still others so blend the characteristic features of several regional aggregates as to make it impossible to place them in any of the varieties with certainty.

It should be borne in mind that any subdivision of this complex species must be in part somewhat artificial. *Eriophyllum lanatum* appears to be a plexus, with many interlacing lines of development running through it. Whether it is a primitive group whose forms have not yet become well defined, because of their recency, or whether it is a plexus formed by the "swamping" (through hybridization) of formerly distinct species, is not known. Whatever their origin, wherever the ranges of two varieties meet or overlap, there arises a host of individuals exhibiting the characters of both, in all conceivable proportions and combinations, and occasionally still other characters not apparent in either. To which of two adjacent geographical units such individuals shall be assigned becomes very largely a matter of individual judgment. Not a few such small groups have been described as new species, which in no way clarifies their relation to the rest of the genus, and gives a disproportionate view of their relative importance.

The author's view in considering this genus is well summed up in the following quotation from Hall (1923):

> What is now needed is not the further increase of such segregates, easy to discover and describe by the thousand, but the organization of this chaotic mass into natural groups. The method of the segregator is to take the scattered and broken twigs of the evolutionary tree and catalogue them without concern as to their origin and relationship, while the true method of taxonomy is to deal with the tree as a whole, and to regard the units in it as so much correlated evidence of evolution.

The writer exposes himself to criticism by attempting a key to these often rather vaguely defined subunits. It seems impossible to construct a key which will allow for all the extreme variants in each region, for no "key-characters" would then be available for use. A positive effort has been made to exclude such common variables as habit, size, form and division of leaves, ray color, and the like, but even this could not be carried out completely without excluding certain important local races.

The author directs attention to three points in the use of this key: (*a*) The key is to the *mean* of each group, and some extreme variants will not be successfully covered. (*b*) For effective determination, it is preferable (often necessary) to have *a small series of specimens* from any given locality. This precaution will frequently eliminate confusion caused by ecological forms, and aberrant specimens in particular, and will tend to show the range of variation in a given local race. (*c*) The key is only an artificial mechanism to facilitate rapid identification of specimens, and one must always *refer to the descriptions* when the key proves ineffective.

1*a*. **Eriophyllum lanatum** var. **typicum** Constance

Actinella lanata, Pursh, Fl. Sept. Am., 560. 1814.
Trichophyllum lanatum, Nuttall, Gen., 2:167. 1818.
Actinea lanata, Steudel, Nom. Bot. Phan., 15. 1821.
Helenium lanatum, Sprengel, Syst., 3:574. 1825.
Eriophyllum caespitosum, Douglas, Lindley, Bot. Reg., 14:1167. 1828.
Eriophyllum lanatum, Forbes, Hort. Woburn., 183. 1833.
Bahia lanata, De Candolle, Prodr., 5:657. 1836.
Bahia leucophylla, De Candolle, *l. c.*
Helenium caespitosum, Steudel, Nom. Bot., ed. 2, 1:733. 1841.
Bahia lanata var. *tenuifolia,* Torrey & Gray, Fl. N. Am., 2:376. 1842.—Not *Bahia tenuifolia* DC., 1836.
Eriophyllum pedunculatum, Heller, Torrey Bot. Club Bull., 25:270. 1898.
Eriophyllum Harfordii, Rydberg, N. Am. Fl., 34:90. 1915.
Eriophyllum superbum, Rydberg, *l. c.*, p. 93.
Eriophyllum lanatum var. *leucophyllum,* Carter et al., Prelim. Cat. Fl. Vancouver & Queen Charlotte Is., Prov. Mus., Victoria, B. C. 1921.
Eriophyllum lanatum var. *typicum* Constance, Proc. Nat. Acad. Sci., 20:413. 1934.

KEY TO THE VARIETIES OF ERIOPHYLLUM LANATUM

A Tube of disk-corollas glabrous.....................................f. var. *Hallii.*
AA Tube of disk-corollas conspicuously glandular or glandular-hairy.
  B Low (usually caespitose) plants, mostly less than 2 dm. high; involucres campanulate, of 6–8 (rarely 10) chartaceous bracts, tending to become discrete; rays 6–8 (rarely 10).....................................h. var. *integrifolium*
  BB Larger plants, mostly 2–10 dm.; involucres hemispheric (or nearly so), of 8–15 subcoriaceous overlapping bracts; rays 8–15.
    C Leaves not pinnatifid, equally tomentose on both surfaces; margins plane.
      D Achenes hairy; ligules oblong; Klamath region...........j. var. *lanceolatum*
      DD Achenes glabrous; ligules oval; mountains of southern California........... i. var. *obovatum*
    CC Leaves less tomentose above than beneath (the upper surface often glabrate and green); margins usually revolute.
      E Pappus reduced to a crown, the teeth mostly shorter than areole.
        F Leaves loosely floccose beneath; coastal plants......d. var. *arachnoideum*
        FF Leaves silky-lanate beneath; Sierran plants..............e. var. *croceum*
      EE Pappus various, but exceeding areole.
        G Basal caudex strongly suffruticose and spreading; plants of high elevations, 4000–7000 feet.............................g. var. *cuneatum*
        GG Rootstock short and less conspicuously woody; mostly plants of lower altitudes.
          H Achenes short, turbinate; ligules 8–10 mm. long..b. var. *achillaeoides*
          HH Achenes elongate, tapering gradually; ligules 10–20 mm. long.
            I Achenes club-shaped, appressed-pubescent; peduncles mostly 1–3 dm. long; Californian....................c. var. *grandiflorum*
            II Achenes narrowly oblong, glabrous; peduncles mostly 3–10 cm.; Pacific Northwest..........................a. var. *typicum*

Herbage clothed throughout with loose tomentum, usually deciduous from stems, involucres and upper leaf-surfaces in age. Stems few to numerous, rather stout, 1–6 dm. high, erect or decumbent at short woody base; simple or corymbosely branched above. Leaves membranaceous or thin, alternate or some opposite, 2–6 cm. long; extremely variable in size, form, and degree of division. Cauline leaves oblong-lanceolate to obovate in outline, pinnatifid into oblong obtuse (rarely acute) divisions, lobes entire, toothed or lobed (or leaves merely incisely lobed, toothed or, rarely, all entire). Lowermost leaves frequently spatulate or oblanceolate, entire to lobed; uppermost, usually narrow and nearly entire. Undersurfaces persistently white-woolly, but usually green and glabrate above; margins revolute. Heads showy, terminal, solitary or loosely corymbose (in latter case, usually smaller). Peduncles stoutish, 5–10 cm. long, not infrequently swollen beneath heads. Involucres hemispheric, loosely floccose or glabrate, 8–10 mm. high, 10–12 mm. broad, of 8–12 linear- to lanceolate-ovate, acute, carinate bracts, strongly overlapping, distinct (or slightly united at base), tips reflexed. Rays 8–12 (sometimes wanting), oblong ligules golden-yellow, 10–20 mm. long, 3–5 mm. wide, toothed at apex. Disk-florets 3–4 mm. long, tube glandular-hairy. Achenes 3–4 mm. long, oblong (or sometimes narrower), tapering gradually toward base, angled, striate, muriculate, glabrous. Pappus variable, of 4–10 oblong, obtuse, erose paleae, less than 1 mm. in length, or some prolonged, linear-lanceolate, acute, 1–2 mm. long.

Range.—Southern British Columbia to southern Oregon, common west of the Cascade divide; thence eastward (along the Columbia River and its tributaries), through eastern Washington and Oregon, to northern Idaho and southwestern Montana; from near sea level to 3000 or 5000 feet.

Lewis' specimens, the type of Pursh's description, were collected near the extreme eastern end of the range. Plants from the Pacific Coast (*E. caespitosum* Dougl.) differ from these in possessing a less persistent tomentum. The former is well represented by the following:

J. B. Leiberg 1066, Coeur d'Alene Mts., Idaho, 1895 (P, RM, S, UC, WSC); *Epling & Houck* 9653, north fork Clearwater River, Idaho, 1929 (UCLA); *J. E. Kirkwood* 1336, Lolo, Montana, 1921 (CAS); *Sandberg et al.* 180, Clearwater River, above Lewiston, Idaho, 1892 (CAS, O, P, S, UC, WSC); *M. Lewis,* uplands on the Kooskooskee River, 1806 (P: photograph of original collection of *Actinella lanata* Pursh).

Although the description in the Botanical Register appears to apply to var. *arachnoideum* (and has been so interpreted by several authors), Douglas' specimens of his *E. caespitosum* (pl. 1) at Kew are definitely the plant of the Northwest. *E. caespitosum* Dougl., then, must be regarded as a synonym of *E. lanatum* (Pursh) Forbes, since Pursh's specific name has priority of publication by fourteen years, and the two phases described differ in only distinctly minor respects. Representative of the population of the Northwest are:

Constance E45, Salem, Marion Co., Ore., 1933 (CAS, O, RM, UC, UCLA, UW), and E48, Battleground, Clark Co., Wash., 1933 (CAS, O, UC); *D. Douglas,* N(orth) W(est) Am(erica) (KEW: authentic material of *E. caespitosum* Dougl.); *L. F. Henderson* 13,548, Eugene, Lane Co., Ore., 1931 (O, UC); *M. E. Peck* 8632, Port Orford, Curry Co., Ore. (WU); *J. T. Howell* 7575, Campbell River, Vancouver Is., B. C. 1931 (CAS).

Bahia leucophylla DC. (pl. 2) was based on dwarfed specimens of this, with generally smaller structures, and fewer involucral bracts and florets. However, this specific name has since been incorrectly and widely applied to various races of var. *integrifolium*. Howell (1900) and Rydberg (1900, 1915) have retained this specific name (transferring it to *Eriophyllum*), and Howell attributes to it a range from "Alaska to California." The author has been unable to discover any authentic record of the genus occurring north of British Columbia. All specimens from Canada seen can be assigned without hesitation to *E. lanatum* var. *typicum*. Examples:

Neé et Haenke, Nutka et Mullgrave (GENEVA: photograph of original collection of *Bahia leucophylla* DC.); *John Macoun,* Chase River, Vancouver Is., 1887 (CAN), and Yale, B. C., 1889 (CAN).

The phase designated *E. pedunculatum* by Heller is a very striking form, with all the leaves entire, and some of the pappus-paleae nearly 2 mm. long, as represented by the type collection: *Heller & Heller* 3390, Lake Waha, Nez Perce Co., Idaho, 1896 (O, UC, S, WSC). Such intermediates as: *J. B. Leiberg* 1434, Sohons Pass, Idaho, 1895 (P, RM, UC) and Lake Waha, Idaho, 1884 (O), however, with some of the leaves divided and others entire, and the pappus intermediate, connect it with the ordinary mean of var. *typicum*.

Slender plants, with smaller and more numerous heads, and highly dissected leaves, provided the type for *E. superbum* Rydb. Such individuals occur sporadically throughout the range of the variety, and are well within the normal limits of variation. *Bahia lanata* var. *tenuifolia* T. & G. was probably applied to similar plants, found along the Columbia River. Examples:

D. Douglas, ex. Am. bor. occ. (KEW); *E. M. Anderson,* Sahtlam, Vancouver Is., 1915 (BC); *John Macoun,* Oak Bay, Victoria, B. C., 1908 (CAN); *Heller & Heller* 3907, Montesano, Wash., 1898 (RM S, UC, WSC); *Constance* E49, Vancouver, Clarke Co., Wash., 1933 (CAS, O, UC); *H. S. Conard,* Higley's promontory of lake, opposite Quiniault, Wash., 1902 (UC: photograph of type of *E. superbum* Rydb.).

Individuals with discoid heads occur with the normally radiate in at least three of the perennial species of the genus, and in many of the varieties of *E. lanatum,* so this character, alone, is not to be considered of specific or varietal weight. Examples of discoid *E. lanatum* var. *typicum:*

Constance E54, Hood River Co., Ore., 1933 (CAS, O, UC); *J. W. Thompson* 849, Washington Co., Ore., 1926 (S); *T. Howell,* Clackamas Co., Ore., 1904 (O).

The name *E. Harfordii* Rydb. was based on a specimen intermediate between typical *E. lanatum* and one of the races of var. *integrifolium,* which usually possesses glandular achenes (*Bahia gracilis* H. & A.; *E. gracile* Gray). This has been re-collected by the writer under E57, The Dalles (type locality), Wasco Co., Ore. (CAS, O, UC). The plant has the habit of var. *typicum* (with which it grows), but the involucres and achenes of var. *integrifolium*. The leaves, ligules, disk-florets, pappus, and other structures are intermediate in character. Such intermediates are especially common east of the Cascades, where the ranges of the two varieties overlap:

Harford & Dunn 453, Dalles, Ore., 1889 (UC: photograph of type of *E. Harfordii* Rydb.); M. E. Peck 9940, DeMoss Springs, Sherman Co., Ore., 1921 (S, WU); *J. B. Leiberg* 170, Pine Creek, Gilliam Co., Ore., 1894 (O); *L. F. Henderson* 5271, Canyon Creek, above Canyon City, Grant Co., Ore., 1925 (CAS, O); *D. Douglas,* Columbia River, Northwest America, 1830 (KEW).

It is of interest to note that Douglas collected the type specimen of var. *integrifolium,* material of var. *typicum,* and specimens interconnecting the two. The two extremes were described as new, but the intermediate plants were not recognized as such.

Shade forms, or semishade forms, often possess large, very thin leaves, the divisions of which are broader than is normal for var. *typicum,* and present a superficial resemblance to those of var. *arachnoideum:*

Constance E50 (CAS, UC) and E52 (O, UC), *J. W. Thompson* 2728, 1927 (S), and *L. L. Haskin,* 1926 (O), all from the Columbia Gorge.

In addition to overlapping the range of var. *integrifolium* east of the Cascades divide, var. *typicum* shares part of its southern range with var. *achillaeoides.* The transition from the one to the other is so gradual that it is quite impossible to draw a distinct boundary between them, as is well shown in the writer's specimens from southern Oregon:

E69, Douglas Co. (O, UC), E70, Douglas Co. (CAS, O, UC), E72, Jackson Co. (CAS, UC), and E74, Josephine Co. (CAS, O, RM, UC).

Specimens examined.—BRITISH COLUMBIA. Mainland: *James M. Macoun* (1901); *John Macoun* (1889-Yale). Mayne Is.: *James M. Macoun* (1914). Vancouver Is.: *E. M. Anderson* (1915); *J. T. Howell* 7575.

WASHINGTON. San Juan Co.: *Beattie* 3395; *Zeller & Zeller* 864. Whatcom Co.; *Henderson* (1892); *Piper* 2802. Skagit Co.: *Gardner* (1895); *St. John* 7901. Island Co.: *Gardner* (1897); *J. W. Thompson* 6043. Clallam Co.: *Elmer* 2605; *Parks & Parks* 0666. Gray's Harbor Co.: *Conard* (1902-photo.); *Heller & Heller* 3907. Mason Co.: *Henderson* (1892); *Piper* 515. King Co.: *Grainger* 267; *Piper* (1883). Pierce Co.: *Frye* (1907); *R. W. Thompson* (1894). Lewis Co.: *J. T. Howell* 7354. Clarke Co.: *Constance* E47, E49. Skamania Co.: *Gorman* 4633. Wahkiakum Co.: *J. R. Anderson* (1918). Chelan Co.: *Otis* 910. Kittitas Co.: *Sharples* 269; *Whited* 410. Klickitat Co.: *Suksdorf* (1881). Walla Walla Co.: *Horner* (1896). Columbia Co.: *Brode* 10; *Darlington* 183. Spokane Co.: *G. N. Jones* 612. Whitman Co.: *Piper* (1894); *Warren & St. John* 3392. Asotin Co.: *G. N. Jones* 978; *Shaw* (1923).

OREGON. Clatsop Co.: *Patterson* 15; *Peck* 13,300. Tillamook Co.: *Peck* 14,619; *J. W. Thompson* 3065. Washington Co.: *J. W. Thompson* 849, 4282. Multnomah Co.: *Constance* E52; *Sheldon* 12,102. Clackamas Co.: *Constance* E46; *Suksdorf* 3327. Yamhill Co.: *Constance* E58; *Lunell* (1903). Marion Co.: *Constance* E45; *Peck* 10,697. Linn Co.: *G. T. Benson* 122; *Constance* E42. Benton Co.: *Constance* E63; *Mason* 2380. Lane Co.: *Constance* E143; *Henderson* 13,548. Douglas Co.: *Constance* E66; *Gale* 190. Josephine Co.: *Constance* E74; *Peck* 7917. Curry Co.: *Peck* 8632, 8816. Hood River Co.: *Constance* E53; *J. W. Thompson* 2911. Wasco Co.: *Constance* E56; *M. E. Jones* (1897). Sherman Co.: *Peck* 9940. Gilliam Co.: *Leiberg* 170, 177. Jefferson Co.:

Henderson (1881-in part). Wheeler Co.: *Gorman* 7633; *Peck* 10,123. Grant Co.: *Henderson* 5271; *Peck* 10,173. Baker Co.: *Cusick* 863 (1881).

IDAHO. Benewah Co.: *Epling & Putnam* 10,276; *Leiberg* 1066. Latah Co.: *Abrams* 837; *Henderson* (1894). Clearwater Co.: *Epling & Houck* 9653. Nez Perce Co.: *Heller & Heller* 3151; *Sandberg et al.* 180. Idaho Co.: *Leiberg* 1434.

MONTANA. Missoula Co.: *Kirkwood* 1336.

1*b*. **Eriophyllum lanatum** var. **achillaeoides** (DC.) Jepson

Bahia achillaeoides, De Candolle, Prodr., 5:657. 1836.
Bahia lanata var. *achillaeoides*, Gray, Bot. Calif., 1:381. 1876.
Eriophyllum caespitosum var. *achillaeoides*, Gray, Proc. Am. Acad., 19:26. 1883.
Eriophyllum achillaeoides, Greene, Man. Bot. Reg. S. F. Bay, 207. 1894.
Eriophyllum ternatum, Greene, Pittonia, 3:185. 1896.
Eriophyllum idoneum, Jepson, Fl. W. Mid. Calif., 524. 1901.
Eriophyllum Greenei, Elmer, Bot. Gaz., 41:313. 1906.
Eriophyllum Cusickii, Eastwood; Rydberg, N. Am. Fl., 34:93. 1915, as a synonym.
Eriophyllum lanatum var. *achillaeoides*, Jepson, Man. Fl. Pl. Calif., 1118. 1925.

Perennial (rarely annual or biennial), herbage tomentose or floccose, but wool usually deciduous from stems and upper leaf-surfaces. Stems few to many, stout or slender, 3–7 dm. tall, from a short, decumbent, woody base, more or less corymbosely branched above. Leaves alternate, some cauline frequently opposite (leaves mostly opposite on seedlings and young shoots), membranaceous, 1–3 cm. long. Basal leaves usually oblanceolate, shallowly lobed, lobes broad; cauline, ovate to deltoid-ovate in outline, 1–2-pinnately or -ternately divided, divisions acute-triangular or linear-subulate, entire, toothed, or lobed. Densely and persistently white-tomentose or -floccose beneath, loosely floccose or glabrate and green above; margins revolute. Heads numerous and corymbosely collected (or fewer, or solitary, and larger) at ends of branches. Peduncles usually slender, 3–10 cm. long. Involucres tomentose, hemispheric, 6–8 mm. high, 8–10 mm. broad, of 9–13 lanceolate or ovate-lanceolate, acute, carinate bracts, strongly overlapping but distinct (or slightly united at base), tips reflexed. Rays 9–13 (sometimes wanting), oval or oblong ligules yellow, 6–9 mm. long, 2–4 mm. wide, toothed at apex. Disk-florets 2.5–3 mm. long, tube glandular-hairy. Achenes cuneate-oblong, short (2.5–3 mm.), muriculate, hispidulous with short white hairs, or glabrous. Pappus variable, but usually of 6–10 short, obtuse, erose paleae, or some longer, but all commonly less than 1 mm. long.

Range.—Northern California, south through the Coast Ranges to Mt. Diablo, Arroyo Mocho, and Loma Prieta Peak; uncommon in the Sierra Nevada, but occurring as far south as Mariposa Co.; north into southern Oregon, from Curry and Douglas counties to Harney Co.; 100–3500 or 4000 ft.

The typical race is the common one of the north Coast Ranges, with leaves pinnately divided, heads loosely corymbose, stems and peduncles rather stout, and achenes more or less hispidulous, as represented by:

Constance E92 (CAS, O, RM, UC) and E93 (C, CAS), Vaca Mts., Solano Co., and E94 (CAS, O, RM, UC, UCLA), E99 (O, RM, UC), and E100 (CAS, O, UC), Mt. Diablo, Contra Costa Co.; *L. R. Abrams* 12,284 (S) and *H. E. McMinn* 956 (S), Napa Co.; *Abrams* 12,524 (S) and *A. A. Heller* 13,126 (CAS, S), Lake Co.

E. idoneum Jepson is based on plants from the Vaca Mountains, with numerous heads and leafy, much-branched stems, which appear to be annual or biennial: *W. L. Jepson* 14,451, ridges below Collin's Camp, Vaca Mts., Solano Co., Calif., 1892 (JEPSON: type). The collection, *A. D. E. Elmer* 4335, Mocho Cr., Alameda Co., Calif., 1903 (CAS, O, P, S, UC-isotypes), the basis for that collector's *E. Greenei,* is a rather large example of the typical race of var. *achillaeoides*, with few and larger heads, but differing from the mean in no important particulars.

The Klamath (Siskiyou) region of California and Oregon supports a somewhat different population, characterized by more slender and less leafy stems, some or most of the opposite cauline leaves ternately (rather than pinnately) dissected, and achenes usually nearly glabrous. This was distinguished by Greene as *E. ternatum,* and by Eastwood as *E. Cusickii.* Extreme examples of the Coast Ranges population, compared with those of the Klamath race, appear strikingly different, but the one passes into the other so gradually that the writer has been unable to draw a demarcation between them. None of the obvious characters by which one would distinguish the extremes seems to be dependable. The Klamath phase is illustrated by the following:

Constance E72 (O, UC), E76 (O, UC), and E119 (CAS, O, UC), Douglas and Josephine counties, Ore., and Siskiyou Co., Calif., respectively; *W. Cusick* 2832, Klamath Falls, 1902 (CAS, O, S, UC, WSC); *M. E. Peck* 14,962 (S, WU), and 9279 (S, WU), from Central Pt. and Ashland, Jackson Co., Ore., 1920; *G. D. Butler* 1279, 1399, 1532 (CAS, S, RM, UC), from Siskiyou Co., Calif., 1910; *Mrs. R. M. Austin* 59, Ashland, Ore., 1893 (UC: type collection of *E. ternatum* Greene).

A series of specimens collected in the redwood belt (Sonoma Co. to Del Norte Co., Calif.) shows a number with broader leaves, resembling those of var. *arachnoideum*. These are probably semishade forms:

Constance E30 (CAS, O, RM, UC), E32 (C, CAS), and E33 (CAS, O, RM, UC), Mendocino Co., and E34, Humboldt Co. (CAS, UC); *J. P. Tracy* 2609, 3268, 3837½, and 4338, Humboldt Co. (UC).

What is perhaps a local race, occurring with the common form in Mendocino and Sonoma counties, is characterized by the possession of leaves with larger, fewer, and usually blunt lobes and glabrous achenes. This so closely approximates var. *typicum* that it has led to a faulty conception of the range of the latter. Examples of this apparently local race:

Constance E25 (CAS, O, RM, UC), Sonoma Co., and E27 (CAS, O, RM, UC) and E29 (CAS, O, RM, UC, W), Mendocino Co., Calif.

Near the summit of the Siskiyou Mountains, both in Oregon and in California, the writer discovered unusually tomentose plants, with little-divided leaves, and a few large heads:

Constance E80 (CAS, O, UC) and E82 (CAS, O, UC), Jackson Co., Ore., 1933.

M. F. Gilman 593 (UC) and 626 (UC) are specimens from Modoc County, with heads fully 3 cm. broad, but otherwise normal. Also in the Klamath region, dwarfed plants are frequent, in which the pinnation of the leaves is partly or wholly suppressed, so that the leaves become lanceolate and serrate; the tomentum is often more persistent; and frequently only one large head develops, instead of the usual several. In the writer's opinion, these modifications are only those to be expected in unfavorable environments. Examples:

L. R. Abrams 8592, Del Norte Co., Calif., 1922 (S), and 8637, Josephine Co., Ore., 1922 (S); *J. W. Thompson* 4639, Josephine Co., Ore., 1928 (S).

On the coastal side *E. lanatum* var. *achillaeoides* intergrades to var. *arachnoideum;* on the landward side, to var. *grandiflorum;* and, at the northern boundary of its range, to var. *typicum.* The distinctions between vars. *achillaeoides* and *grandiflorum* are very poor, depending chiefly upon characters of size and number of structures, criteria which are notoriously undependable. Particularly in the Klamath area, the indigenous varieties of *E. lanatum* intermingle so confusedly that it seems quite impossible to assign many specimens definitely to any one subspecific category.

Specimens examined.—OREGON. Douglas Co.: *Constance* E72; *Henderson* 12,955. Josephine Co.: *Abrams* 8637; *Constance* E77. Curry Co.: *Henderson* 5905; *Peck* 4372. Jackson Co.: *Constance* E80; *Constance & Henderson* E133. Klamath Co.: *Constance* E123; *Constance & Henderson* E137. Lake Co.: *Constance & Henderson* E141; *Ferris & Duthie* 326. Harney Co.: *Henderson* 8557; *Leiberg* 2415.

CALIFORNIA. Del Norte Co.: *Eastwood* 10,279; *Kildale* 8481. Humboldt Co.: *Constance* E34; *Tracy* 3268. Siskiyou Co.: *Constance* E119; *Kildale & Gillespie* 8031. Modoc Co.: *Ferris & Duthie* 60; *Gilman* 593. Shasta Co.: *Hall & Babcock* 4250; *Peirson* 10,305. Lassen Co.: *Bowerman* 2385; *Peirson* 6849. Mendocino Co.: *Constance* E30; *Davy & Blasdale* 5072. Sonoma Co.: *Constance* E25; *Parks & Parks* 0837. Glenn Co.: *Constance* E12; *Heller* 11,527. Lake Co.: *Abrams* 6282; *Heller* 13,126. Colusa Co.: *Ferris* 6445; *Heller* 12,353. Yolo Co.: *C. F. Baker* 2934; *Jepson* 8958. Napa Co.: *Constance* 138; *McMinn* 956. Solano Co.: *Constance* E92; *Jepson* 7195. Contra Costa Co.: *Bowerman* 2267; *Constance* E100. Alameda Co.: *Elmer* 4335. Santa Cruz Co.: *Mexia* (1926). Butte Co.: *Keifer* (1928). Plumas Co.: *Clemens* (1920). Nevada Co.: *Dudley* (1893); *Eastwood* 554. Placer Co.: *L. E. Smith* 1831. El Dorado Co.: *Hall* 11,292. Calaveras Co.: *Blaisdell* (Mokelumne Hill). Tuolumne Co.: *Constance* E106; *Jepson* 7688. Mariposa Co.: *Congdon* (1895); *Wolf* 4860.

1c. Eriophyllum lanatum var. grandiflorum (Gray) Jepson

Bahia lanata, Bentham, Pl. Hartweg., 317. 1849.—Not *Bahia lanata* DC., 1836.
Bahia lanata var. *grandiflora*, Gray, Bot. Calif., 1:381. 1876.
Eriophyllum caespitosum var. *grandiflorum*, Gray, Proc. Am. Acad., 19:26. 1883.
Eriophyllum speciosum, Greene, Erythea, 1:149. 1893.
Eriophyllum grandiflorum, Greene, Fl. Franc., 443. 1897.
Eriophyllum lanatum var. *grandiflorum*, Jepson, Fl. W. Mid. Calif., 524. 1901.
? *Egletes Californicus*, Kellogg, Proc. Calif. Acad., 1:56. 1855.

Densely white-tomentose throughout in juvenile state, tomentum more or less deciduous from stems and upper leaf-surfaces. Stems several, stout, 3–10 dm. high, erect or decumbent at short woody base, leafy below; the larger freely branched above, the smaller simple. Leaves alternate (or some opposite), membranaceous, linear to lanceolate or oblanceolate, 3–8 cm. long; entire, or laciniately toothed or pinnatifid, lobes linear and acute (or oblong and obtuse), entire or toothed; persistently white-tomentose beneath, floccose or glabrate above; margins revolute. Heads solitary at ends of stems or branches. Peduncles stout, 1–3 dm. long, often swollen under heads. Involucres hemispheric, densely and persistently white-woolly, 8–10 mm. high, 10–15 mm.

broad, of 10–15 lanceolate (or oblong-ovate), acute, carinate bracts, strongly overlapping and distinct or united at base, tips reflexed. Rays 10–15 (sometimes wanting), narrowly oblong ligules yellow, 10–15 mm. long, 4–6 mm. wide, toothed at apex. Disk-florets 4 mm. long, tube glandular-pubescent. Achenes 4 mm. long, clavate-linear, sharply 4-angled, more or less appressed-pubescent, with soft tawny hairs (or nearly glabrous). Pappus variable, but typically of 8–12 unequal, linear-oblong or lanceolate paleae, mostly acute and all erose, the longer 1 mm. or more long.

Range.—Sierra Nevada foothills (Mariposa Co. to Placer Co., California), throughout the Sacramento and upper San Joaquin valleys to Siskiyou, Humboldt, and Del Norte counties; 100–4000 feet.

The characters of this variety are rather unstable, their distinctness depending chiefly upon size, which is very plastic under environmental influence. This is well shown in the writer's E103*a* and E103*b*, Tuolumne Co., 1933 (CAS, UC), in which the greatest extremes of habit, leaf-form and division, and of size and number of parts are exhibited in plants belonging to the same colony and growing within a few feet of each other.

In general, var. *grandiflorum* may be distinguished from its nearest relative, var. *achillaeoides*, by its larger size, longer peduncles, larger heads, longer, narrower, and less divided leaves, more numerous and narrower involucral bracts, more numerous rays, more slender achenes, with a characteristic soft pubescence, and better developed and more slender pappus. However, none of these characters manifests a high degree of constancy, and the variations are often not concomitant, so that many specimens appear to belong as much to one variety as to the other:

A. A. Heller 11,366, Marysville Buttes, 1914 (UC), and 11,354, Glenn Co., 1914 (S, UC); *R. S. Ferris* 673 (S) and 6322 (S), Sutter Co.: *C. B. Wolf* 5117, Bagby, Mariposa Co., 1933 (RSA).

The common valley plant is well represented by the following large, much branched specimens:

Heller & Brown 5483, Berry Canyon, Butte Co., 1902 (S, RM, UC); *A. A. Heller* 10,763, Table Mt., Butte Co., 1913 (S), and 12,446, between McCloud & Sacramento rivers, Shasta Co., 1916 (CAS, S); *Constance* E103*b* and E104, Tuolumne Co., 1933 (CAS, UC).

Smaller plants, but otherwise typical, are these:

Constance E90 and E91, Shasta Co., 1933 (CAS, O, UC), and E118, Tehama Co., 1933 (CAS, O, RM, UC, UCLA, UW); *Hall & Babcock* 4005, Pit River Canyon, 1903 (UC, RM, S); *H. M. Hall* 10,147, Rocklin, Placer Co., 1916 (S, UC).

The Sierran foothill variant, *E. speciosum* Greene, has slightly broader leaves, less dense tomentum, and all structures slightly smaller in proportion: *G. Hansen* 912, Agric. Sta., and 1144, Armstrong's Sta., both Amador Co., 1895 (S, UC). This is, however, quite indistinguishable from many of the valley plants. Members of this variety, in the Sierra Nevada, become progressively reduced in size and number of all structures as higher altitudes are attained, and appear to pass into vars. *croceum* and *cuneatum* by an unbroken transition.

Palmer's specimen from Guadalupe Island, off the coast of Lower California, 1875 (GRAY), is the only known material from that region and probably the only existing collection of *E. lanatum* from any of the Californian islands. It is fairly well matched by such a specimen as *Hall* 10,147, already cited. The Palmer specimen is about 3.5 dm. tall, with 7 erect, simple stems arising from a short, woody, decumbent base. The leaves (numerous on the lower portion of the stems) are narrowly linear-lanceolate and acute, 2–3 cm. long; the lower toothed or lobed divisions narrow and acute; the uppermost, smaller and entire; densely white-tomentose below, -floccose above. The involucres are densely white-tomentose, 10 mm. high, 15 mm. broad, of about 13 bracts (of the usual form). Rays are the same number. Achenes are rather short, broad, and nearly glabrous (more like var. *achillaeoides*), and the pappus is shorter than typical. However, there is (on the basis of this sole material) nothing sufficient to separate this plant from var. *grandiflorum*. The writer is at a loss to explain this peculiar distribution, except to suggest that the Guadalupe specimen may represent a relict of a formerly much more numerous population.

Individuals with discoid heads are not uncommon, as exemplified by the specimens:

A. A. Heller 11,354, Orland, Glenn Co., 1914 (S, UC), and 11,435, Alder Springs, Glenn Co., 1914 (S, UC).

An extremely ambiguous species, *Egletes Californicus* Kellogg, should be mentioned here. Curran (1885) tentatively referred it to *E. caespitosum*, and, if it falls in this genus at all, it is probably close to *E. lanatum* var. *grandiflorum*.

Specimens examined.—CALIFORNIA. Siskiyou Co.: *Constance* (1928-Weed); *Jepson* 14,571. Del Norte Co.: *Kildale* 9913. Humboldt Co.: *Chandler* 1301; *Tracy* 2695. Trinity Co.: *Tracy* 4285; *Yates* 346. Shasta Co.: *Constance* E87; *Hall & Babcock* 4005. Glenn Co.: *Heller* 11,354, 11,435. Tehama Co.: *Constance* E118; *Jepson* 14,574. Colusa Co.: *Ferris* 587, 6411. Butte Co.: *C. F. Baker* 3275; *Heller & Brown* 5483. Sutter Co.: *Ferris* 673; *Heller* 11,366. Yolo Co.: *Ferris* 714. Yuba Co.: *Cramsie* (1923); *Eastwood* 10,539. Sierra Co.: *V. Jones* (1920). Plumas Co.: *Head* (1920). Nevada Co.: *Hall* 10,171; *Keck* 1605. Placer Co.: *Hall* 10,147; *Hall & Essig* 10,156. El Dorado Co.: *M. E. Jones* 3379; *Vortriede* (1931). Sacramento Co.: *Ramaley* 11,226; Wolf 4971. Amador Co.: *Braunton* 1024; *Hansen* 912. Calaveras Co.: *Davy* 1504; *Stanford* 391. San Joaquin Co.: *Rattan* (1880). Tuolumne Co.: *Constance* E104; *Jepson* 3453. Mariposa Co.: *Jepson* 14,573; *Wolf* 5117.

LOWER CALIFORNIA. Guadalupe Is.: *Palmer* (1875).

1*d*. Eriophyllum lanatum var. arachnoideum (F. & L.) Jepson

Bahia arachnoidea, Fischer & Avè-Lallement, Ind. Sem. Hort. Petrop., 9:63. 1842.
Bahia latifolia, Bentham, Bot. Voy. Sulph., 30. 1844.
Bahia lanata var. *brachypoda*, Gray, Bot. Calif., 1:381. 1876.
Eriophyllum caespitosum var. *latifolium*, Gray, Proc. Am. Acad., 19:26 (in part). 1883.
Eriophyllum arachnoideum, Greene, Man. Bot. Reg. S. F. Bay, 207. 1894.
Eriophyllum lanatum var. *arachnoideum*, Jepson, Man. Fl. Pl. Calif., 1119. 1925.
Eriophyllum Brownii, Eastwood; Jepson, *l. c.*, as a synonym.
? *Eriophyllum trollifolium*, Lagasca, Gen. et Sp., 28. 1816.
? *Helenium trollifolium*, Sprengel, Syst., 3:573. 1825.
? *Bahia trollifolia*, De Candolle, Prodr., 5:657. 1836.

Herbage clothed with long floccose wool, deciduous in age. Stems branched from woody base, 3–6 dm. high. Branches frequently lax and decumbent, very leafy. Leaves alternate (or some opposite), 2–5 cm. long, broad and thin; rhombic in outline, or narrowed to oblanceolate, with broadly cuneate, entire base, 3–5-incisely lobed or decurrently pinnatifid at, or above, middle; lobes oblong or triangular, mostly obtuse, entire or sinuately dentate (or incised); loosely floccose beneath, green and glabrate above; margins revolute. Heads solitary or several, on terminal or axillary peduncles. Peduncles 3–10 cm. long. Involucres hemispheric, 8–11 mm. high, 9–15 mm. broad, loosely floccose or glabrate; of 8–15 oblong-ovate, acute, carinate bracts, overlapping, and distinct or united at base. Rays 8–15, oval or oblong ligules golden-yellow (often turning brown in drying), 8–10 mm. long, 3–7 mm. wide; toothed at apex. Disk-florets 3–4 mm. long, tube conspicuously glandular-hirsute. Achenes 3–4 mm. long, turbinate, glabrous, striate and muriculate. Pappus reduced to crown of obtuse, erose teeth, typically shorter than areole, but sometimes slightly longer (sometimes obsolete?).

Range.—Along the coast of central California, in the redwood belt and on seaward hill slopes, from Del Norte Co. to Monterey Co.; most numerous from near sea level to 1000 or (rarely) 2000 feet.

Lagasca's *E. trollifolium,* because of the uncertainty of the place of collection, the early loss of the original specimens, and the fact that the ligulate florets are described as "purpurea" (rays discolored in drying?), has never been satisfactorily identified, and there is little hope that it ever will be. It is referred as a synonym to *E. lanatum* var. *arachnoideum,* only as a bare possibility. The description of *E. caespitosum* Dougl. (1828) agrees with *E. lanatum* var. *arachnoideum,* except that the involucre is represented as strongly gamophyllous. Rydberg (1915) and others have so interpreted this name (*E. caespitosum* Dougl.). However, Douglas' specimens are *E. lanatum* var. *typicum,* of the Northwest, and do not correspond with the description of *E. caespitosum* in respect to habit, foliage, involucres, achenes, or pappus.

Bahia arachnoidea F. & L. is, then, the first undoubtedly authentic name applicable to the Californian coastal plant. It does not appear advisable to separate this entity from the polymorphous *E. lanatum,* since it intergrades freely with var. *achillaeoides,* and is more closely related to the Sierran var. *croceum* than *croceum* is to any of the other varieties.

Occupying chiefly the redwood belt, this is typically a shade plant, with the foliage and lax habit to be expected in such an environment. When it is found in more exposed situations, its characteristic growth form is often appreciably altered. Plants with very large, short-peduncled heads and the leaves thickened from exposure were the basis for the names, *Bahia lanata* var. *brachypoda* Gray, and *E. Brownii* Eastwood, as:

H. E. Brown 776, Mendocino, Mendocino Co., 1898 (RM, UC); *K. Brandegee,* Bodega Point, 1906 (UC).

Individuals occupying dryer hill slopes often have the leaves smaller and more deeply lobed (*A. A. Heller* 8400, Mt. Tamalpais, Marin Co., 1906 [CAS, S, UC]), or the heads smaller and more numerous (*K. Brandegee,* Tamalpais, 1892 [UC]). Extreme development of broad, thin leaves and lax habit is shown in *A. D. E. Elmer* 4549, Point Reyes P. O., Marin Co., 1903 (CAS, O, S, UC).

In the northern part of its range, var. *arachnoideum* becomes confused with vars. *achillaeoides* and *grandiflorum* to produce an exceedingly complex population. In Del Norte and Humboldt counties, especially, occur many plants which the writer, lacking opportunity for sufficient field study, has been unable to assign with certainty to any one of the three, since they combine some of the characters of all. Some specimens, which should perhaps be referred here, exhibit more deeply divided leaves, more numerous and larger heads, and better developed pappus, and in some of these the achenes are provided with a few hairs. Examples:

Davy & Blasdale 5563, 1899 (UC), and *Tracy* 2539, 5082, and 7607 (UC), all Humboldt Co.

In the Synoptical Flora, Gray combined this variety with the following, var. *croceum,* which is almost indistinguishable from it morphologically, but distinctly separated in range.

Specimens described as *E. latilobum* Rydb. appear to be the product of hybridization between *E. lanatum* var. *arachnoideum* and *E. confertiflorum,* and are discussed under the taxonomic treatment of the last-named species.

Specimens examined.—CALIFORNIA. Del Norte Co.: *Abrams* 8371; *Kildale* 3726. Humboldt Co.: *Chandler* 1093; *Davy & Blasdale* 5563. Mendocino Co.: *Abrams & Bacigalupi* 8195; *Eastwood* 11,426. Sonoma Co.: *J. T. Howell* 5292; *M. E. Jones* 2773. Marin Co.: *Elmer* 4549; *Heller* 8400. San Mateo Co.: *C. F. Baker* 797; *McMinn* 258. Santa Cruz Co.: *C. L. Anderson* (Cat. Fl. Pl. Santa Cruz Co., 39. 1893). Monterey Co.: *McLean* (1874).

1e. Eriophyllum lanatum var. croceum (Greene) Jepson

***Eriophyllum caespitosum* var. *latifolium*, Gray, Proc. Am. Acad., 19:26 (in part). 1883.**
***Eriophyllum croceum*, Greene, Erythea, 3:124. 1895.**
***Eriophyllum lanatum* var. *croceum*, Jepson, Man. Fl. Pl. Calif., 1118. 1925.**

Herbage with fine arachnoid wool, more or less deciduous from stems and upper leaf-surfaces. Stems mostly simple, very leafy, 1.5–4 dm. high, often decumbent at short, woody (frequently stoloniferous) base. Leaves alternate (or some opposite), 2–5 cm. long, broad, and thin; narrowly oblanceolate to obovate in outline, with narrow cuneate or oblong entire base; coarsely serrate or lobed at, or above, middle, lobes or teeth short and broad, obtuse or acute, entire or toothed; silky-lanate beneath, green and glabrate above; margins revolute. Heads solitary or several, terminal. Peduncles 3–8 cm. long. Involucres hemispheric, 5–8 mm. high, 10–12 mm. broad, loosely floccose or glabrate, of 10–14 oblanceolate, acute, carinate bracts, overlapping and distinct (or nearly so). Rays 10–14, oblong ligules golden-yellow, 8–10 mm. long, 3–4 mm. wide, toothed at apex. Disk-florets 3–4 mm. long, tube conspicuously glandular-hairy. Achenes 3–4 mm. long, turbinate, glabrous, striate, and muriculate. Pappus reduced to crown of obtuse, erose teeth, shorter than areole (or entirely lacking, especially in rays).

Range.—Western slope of the Sierra Nevada, in the yellow-pine belt, from Butte Co. to Tulare Co., Calif.; mostly 3000–5000 feet.

Morphologically, this variety is very similar to var. *arachnoideum,* but the two are widely separated in range and differ in minor characters of tomentum, leaf form and division, involucres, and the like. It may be of significance that var. *arachnoideum* occurs in the Humid Transition life zone, with *Sequoia sempervirens,* while var. *croceum* occupies the Sierran Transition zone, in company with *Sequoia gigantea.* The structural similarity and parallelism of range between vars. *arachnoideum* and *croceum* point to a common ancestry and a connection with the prehistoric redwood forest. It is not surprising that Gray placed the two together and suggested that the Sierran plants might be intermediate between the coastal population and his *E. caespitosum* var. *integrifolium.*

Specimens from the southern portion of the range sometimes have the leaves more tomentose above, as in:

Hall & Chandler 147, Pine Ridge, Fresno Co., 1900 (S, UC); *K. Brandegee,* Marble Fork of the Kaweah, 1905 (UC); *W. R. Dudley* 1679, Brook's Camp, Upper Kaweah River region, Tulare Co., 1896 (S).

E. lanatum var. *croceum* appears to intergrade with var. *cuneatum* and, perhaps, with other varieties of the same species.

Specimens examined.—CALIFORNIA. Butte Co.: *Heller* 10,806. Nevada Co.: *Eastwood* 514, 555. El Dorado Co.: *Hall* 11,366; *Shockley* (1880). Amador Co.: *Hansen* 1036 (UC: type of *E. croceum* Greene), 1136. Calaveras Co.: *Blaisdell* (Big Trees); *Davy* 1562. Alpine Co.: *Mason* 3335. Tuolumne Co.: *Constance* E107; *Hall & Babcock,* 3396. Mariposa Co.: *J. T. Howell* 430; *Jepson* 14,568. Fresno Co.: *Hall & Chandler* 147; *Wolf* 5042. Tulare Co.: *C. F. Baker* 4513; *Dudley* 1184.

1*f*. Eriophyllum lanatum var. Hallii Constance

Eriophyllum caespitosum, Douglas sensu Coville, Contr. U. S. Nat. Herb., 4:135. 1893.—Not *E. caespitosum Dougl.,* 1828.

Eriophyllum lanatum var. *Hallii,* Constance, Proc. Nat. Acad. Sci., 20:411. 1934.

Perennial, the thinly floccose wool deciduous from stems and involucres in age. Stems numerous, sparingly branched above or simple, rather leafy, 3–4 dm. high; erect from decumbent, loosely caespitose, woody base. Leaves tending to be alternate above and opposite below, broad and thin, 2.5–5 cm. long, ovate in outline; upper sessile, lower petioled, but all pinnately incised or pinnatifid, with pair of well-developed basal lobes; oblong or broadly lanceolate divisions obtuse or acute, entire or toothed; loosely floccose on both surfaces, but glabrate above; margins inconspicuously revolute. Heads solitary or few, terminal, rather small (2 cm. or less in breadth with rays expanded). Peduncles slender, 5–12 cm. long. Involucres nearly hemispheric, floccose to glabrate, 8–10 mm. high, 7–8 mm. broad, of 8–9 oblong-ovate, acute, subcoriaceous, carinate bracts, strongly overlapping (sometimes appearing to be 2-seriate) and slightly united at base. Receptacle convex, foveolate. Rays 8–9, yellow ligules broadly oblong, 10–13 mm. long, 4–6 mm. wide, toothed at apex. Disk-florets numerous (75–100), 4–5 mm. long, tube glabrous (a few scattered, tack-shaped glands visible under 400-diam. magnification), and exceeded by narrowly campanulate throat. Anther-appendages ovate, obtuse. Style-branches obtuse. Achenes narrowly oblong, tapering gradually to base, sharply 4-angled, striate, muriculate, more or less pubescent (nearly glabrous in some) with short white hairs, 4–5 mm. Pappus of 8–12 paleae, either (*a*) unequal, shorter oblong, obtuse, erose, and longer acute, twice as long, or (*b*) subequal, and all lanceolate, longest 1.5–2 mm., exceeding corolla-tube (but this will doubtless prove to be variable).

Range.—This is known only from the type collection, vicinity of Old Fort Tejon (Kern Co., Calif.), Upper Sonoran zone, 3500 feet, June 16–19, 1905, collected by *H. M. Hall* 6262 (UC: type, RM, S), and that of *F. V. Coville & F. Funston* 1184, in the mountains south of Fort Tejon, Kern Co., Calif., July 7, 1891 (USNH).

So far as known, this does not intergrade with any of the other varieties of *E. lanatum,* since it appears to be entirely isolated from all of them. If this isolation proves (when more material has been collected) to be incomplete, intergradation probably will be found to occur. *E. lanatum* var. *Hallii* suggests vars. *arachnoideum* and *croceum,* in foliage. The smaller heads, narrower in-

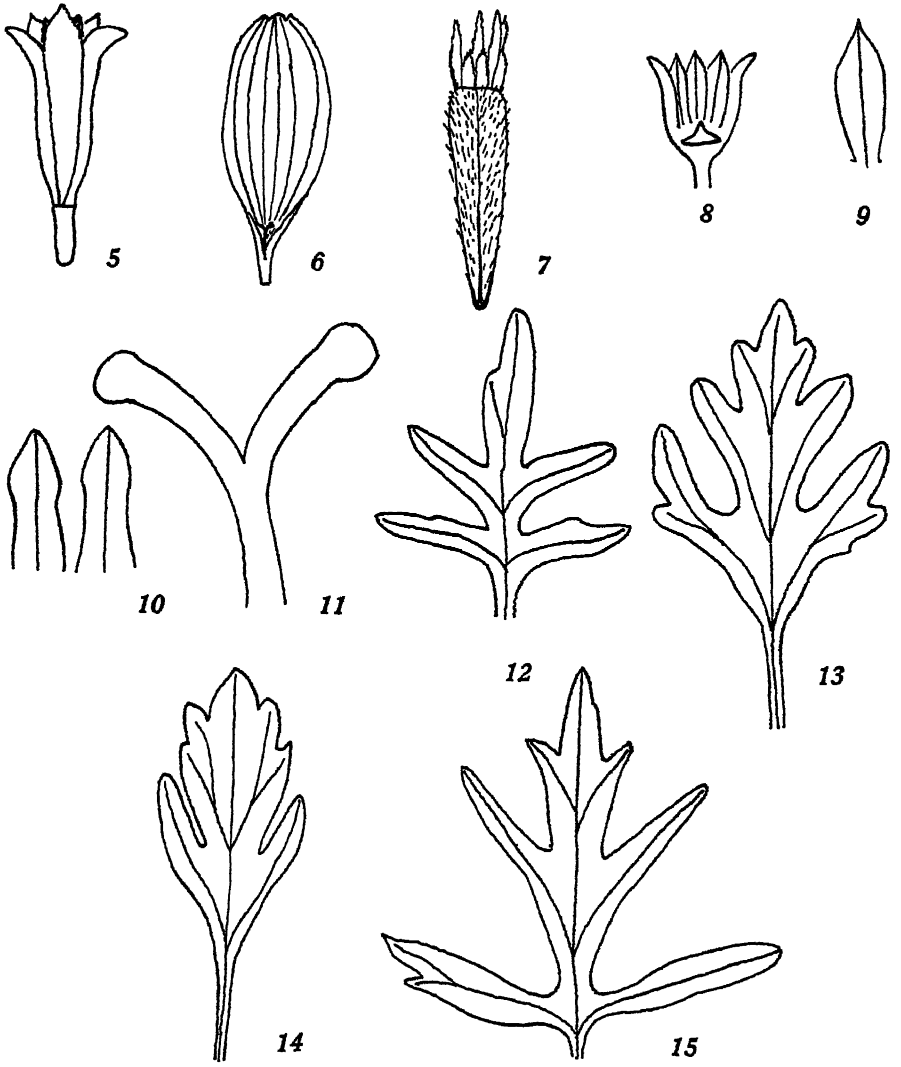

Fig. 5. Disk-corolla. × 7. Fig. 6. Ray-corolla. × 3. Fig. 7. Achene with pappus. × 7. Fig. 8. Longitudinal section through involucre, showing receptacle. × 1. Fig. 9. Involucral bract. × 2. Fig. 10. Apical anther-appendages. × 50. Fig. 11. Style-tips. × 50. Figs. 12–15. Characteristic leaf forms. 12 and 15 × 1, 13 and 14 × ⅓.

volucres, more slender and hairy achenes, well-developed pappus, and the glabrous corolla-tube (unique in the species) separate it adequately from either and from all the other varieties.

1*g*. **Eriophyllum lanatum var. cuneatum (Kell.) Jepson**

Bahia cuneata, Kellogg, Proc. Calif. Acad., 5:49. 1873.
Bahia integrifolia, Gray, Bot. Calif., 1:381 (in part). 1876.—Not *B. integrifolia* DC., 1836.
Eriophyllum caespitosum var. *integrifolium*, Gray, Proc. Am. Acad., 19:26 (in part). 1883.—Not *Trichophyllum integrifolium* Hook., 1833.
Eriophyllum chrysanthum, Rydberg, N. Am. Fl., 34:89. 1915.
Eriophyllum cuneatum, Rydberg, *l. c.*, p. 90.
Eriophyllum Bolanderi, Rydberg, *l. c.*, p. 91.
Eriophyllum Cineraria, Rydberg, *l. c.*, p. 93.
Eriophyllum lanatum var. *cuneatum*, Jepson, Man. Fl. Pl. Calif., 1118. 1925.

Stems numerous, erect, 2–4 dm. high, leafy below, from decumbent, spreading, strongly suffruticose base; floccose or tomentose throughout. Leaves alternate (or some opposite), mostly 2–4 cm. long; basal leaves and those of sterile shoots oblanceolate to obovate in outline, tapering into cuneate or oblong base, coarsely toothed or 3–5-lobed; cauline, mostly narrower, lanceolate, but ovate in some, toothed or 3–5-lobed, or smaller entire; teeth or lobes short and acute, or larger obtuse, entire or toothed; persistently white-tomentose below, floccose or glabrate above; margins revolute. Heads solitary, terminal. Peduncles 5–10 cm. long. Involucres nearly hemispheric, tomentose, 8–10 mm. high, 8–12 mm. broad, of 8–14 linear-lanceolate, acute, carinate bracts, overlapping and distinct (or slightly united at base). Rays 8–14, oblong ligules golden-yellow, 8–10 mm. long, 2–4 mm. wide. Disk-florets about 4 mm. long, tube glandular-hairy. Achenes 3–4 mm. long, clavate-linear, glabrous to hairy (not infrequently in same head). Pappus also variable: (*a*) of 8–12 unequal, oblong or lanceolate, obtuse or acute, erose paleae, longest 1–2 mm. long; (*b*) all obtuse and subequal, and less than 1 mm.

Range.—Northern Sierra Nevada, 4000–7000 feet, from Placer Co. north to Butte and southeastern Lassen counties; thence eastward to Washoe Co., Nevada.

These plants are confusingly variable in foliage, and in achene and pappus characters, and possibly do not form a natural grouping, but the individuals included appear to be closely related to one another, and all are narrowly confined to the same phytogeographic area. They seem to intermingle the characters of all the other varieties which are to be found in proximity to this region: vars. *croceum*, *integrifolium*, *grandiflorum* and, perhaps, *achillaeoides*.

The segregates of the North American Flora are based upon highly variable characters, as follows: *E. chrysanthum*—leaves oblanceolate, serrate, or 3-lobed, achenes hirsute, pappus paleae scarcely 1 mm. long; *E. cuneatum*—leaves oblanceolate, 3–5-lobed, achenes glabrous, paleae less than 0.3 mm. long; *E. Bolanderi*—leaves cuneate-obovate, 3–5-lobed or 3-cleft, achenes sparingly hirsute, paleae fully 1 mm.; *E. Cineraria*—basal leaves spatulate, cauline narrower, 3–5-lobed, achenes glabrous, paleae about 0.5 mm.

Using only such criteria, it would be easy to make an indefinite number of equally valueless segregates from any large series of specimens. Leaf shape and division seem to depend chiefly upon size. This is well shown in the writer's specimens from Plumas County: E114 (CAS, O, UC), E115 (CAS, O, UC), E116 (CAS, O, RM, UC, UCLA), and E117 (CAS, O, UC), in which the larger leaves of stems from the same rootstock show the "Cineraria-type" of structure, and the smaller, the "chrysanthum-type." Glabrous and pubescent achenes are found in the same heads in some specimens, as *H. M. Hall* 8744, Cisco, 1910 (S, UC), which would suggest that this character is also unreliable. *E. Bolanderi* Rydb. is known from a single collection at "Bear Valley," which here is probably Nevada County. It is peculiar for its deeply cleft stem leaves, but its affinities are undoubtedly here.

All these segregates agree in the following characters: the possession of a strongly suffruticose, spreading, and decumbent base; the linear-lanceolate bracts of the narrowly hemispheric involucre; and the clavate-linear, sharply 4-angled achenes; and all occur in the same area. In the author's opinion, they should be kept together and, accordingly, he has expanded the oldest name to include them all, following Jepson in reducing this to varietal status. This variety cannot well be detached from *E. lanatum,* since it intergrades with other varieties of that species, as mentioned above.

Specimens examined.—CALIFORNIA. Lassen Co.: *Brandegee* (1892). Plumas Co.: *Constance* E115; *Heller* 10,855 (UC: type collection of *E. chrysanthum* Rydb.); *Heller & Kennedy* 8849 (UC: type collection of *E. Cineraria* Rydb.). Butte Co.: *Heller* 12,821. Nevada Co.: *Bolander & Keller* (1872) (UC: photograph and fragment of type of *E. Bolanderi* Rydb.); *M. E. Jones* 2491. Placer Co.: *Hall* 8744; *Walker* 1279.

NEVADA. Washoe Co.: *Kennedy* 21.

1*h*. Eriophyllum lanatum var. integrifolium (Hook.) Smiley

Trichophyllum integrifolium, Hooker, Fl. Bor. Am., 1:316. 1833.
Trichophyllum multiflorum, Nuttall, Jour. Acad. Phila., 7:35. 1834.
Bahia integrifolia, De Candolle, Prodr., 5:656. 1836.
Bahia gracilis, Hooker & Arnott, Bot. Beechey Voy., 353. 1838.
Bahia multiflora, Nuttall, Trans. Am. Philos. Soc., ser. 2, 7:373. 1841.
Eriophyllum caespitosum var. *integrifolium,* Gray, Proc. Am. Acad., 19:26 (in part). 1883.
Eriophyllum caespitosum var. *leucophyllum,* Gray, *l. c.*—Not *Bahia leucophylla* DC., 1836.
Eriophyllum gracile, Gray, *l. c.*
Eriophyllum Watsoni, Gray, *l. c.*
Eriophyllum integrifolium, Greene, Fl. Franc., 444. 1897.
Eriophyllum leucophyllum, Rydberg, Mem. N. Y. Bot. Gard., 1:422. 1900.—Not *Bahia leucophylla* DC., 1836.
Eriophyllum multiflorum, Rydberg, *l. c.*
Eriophyllum lutescens, Rydberg, N. Am. Fl., 34:87. 1915.
Eriophyllum monoense, Rydberg, *l. c.,* p. 87.
Eriophyllum trichocarpum, Rydberg, *l. c.,* p. 89.
Eriophyllum nevadense, Gandoger, Bull. Soc. Bot. France, No. 65:40. 1918.
Eriophyllum lanatum var. *integrifolium,* Smiley, Univ. Calif. Publ. Bot., 9:378. 1921.
Eriophyllum lanatum var. *monoense,* Jepson, Man. Fl. Pl. Calif., 1119. 1925.

Herbage persistently tomentose, canescent, or floccose. Stems numerous, 1–2 (rarely 3–4) dm. high, taller very slender; simple (sometimes sparingly branched), erect from suffruticose base, or short caespitose caudex. Leaves soft, thickish or thin, never coriaceous, 1–4 cm. long; lower oblanceolate, cuneate or obovate, entire or (more often) 3–5-toothed or -lobed at apex; cauline narrower, linear-oblanceolate to ovate in outline, entire, toothed or lobed (sometimes 3-cleft or pinnatifid, with linear divisions); white- or yellowish-tomentose on both sides (sometimes canescent), or upper surface floccose and greenish; margins plane. Peduncles 3–10 cm. long. Involucres campanulate, 6–8 mm. high, 6–10 mm. broad, usually floccose. Bracts 5–8 (rarely 10), oblong to elliptic, acute or obtuse, carinate, little overlapping and tending to become discrete (especially under pressure), quite distinct; tips erect. Rays 5–8 (occasionally 10), yellow ligules oval or oblong, 6–10 mm. long, 2–5 mm. wide. Disk-florets few (20–60?), about 4 mm. long, tube glandular or glandular-hairy. Receptacle nearly flat to subconic. Achenes club-shaped (rarely broader), glabrous, hairy, glandular or glandular-hairy, two or more states frequently in same head. Pappus extremely variable, of 8–12 paleae which are: (*a*) unequal, oblong-linear, obtuse, erose, longest about 1 mm.; (*b*) slender, lanceolate, 1–2 mm., equal to very unequal; (*c*) short, obtuse, erose, subequal, distinctly less than 1 mm.

Range.—Columbian Plateau, from the Cascade-Sierran summit on the west, to the Yellowstone Plateau (and adjacent Rocky Mts.) on the northeast, to the ranges of the Canadian boundary on the north, and south into the northwestern edge of the Great Basin and down the high Sierra Nevada (to Inyo Co., Calif., and adjacent Nevada); 3500 (in the northern part of its range) to 10,000 feet, and occasionally higher.

This is the montane and plateau variant of the species, a complex population of low and usually caespitose plants, embracing strikingly diverse individuals. The characters, however, appear in such a variety of combinations that the author has been unable to work out a practical basis for the segregation of minor units. It is not surprising that various systematists have designated many of the extremes by binomials. Many such descriptions were made upon scanty or fragmentary material, which gives no idea of the prevalent variation, and few of the authors knew the living plants in the field. These and subsequent workers have attempted to segregate the population about these described landmarks, with the chaotic result evidenced in the synonymy.

The plants are small, with characteristically simple, monocephalous or sparingly branched stems. The campanulate involucres of chartaceous, little overlapping bracts, although numerous intergrades occur, set them apart from the other forms of *E. lanatum*. Leaf form and division, nature of achene surface, and condition of the pappus are all highly variable. Not infrequently, such instability extends to a single plant, which will exhibit several states of one or more of the structures in question, entitling it to admission to several of the described specific categories.

The characters which have been given most diagnostic weight (Gray, 1876, 1883, 1884; Rydberg, 1915) are the following, in the order listed: (*a*) nature of achene surface; (*b*) entirety or division of leaves; and (*c*) length of pappus. In the accompanying chart (fig. 16), the supposedly critical states of these characters are shown on the abscissa of the graph, and on the ordinate, the number of specimens examined, placed in relation to these criteria. For pappus length, approximately 1 mm. has been arbitrarily chosen as "medium";

distinctly less than 1 mm., "short"; 1.25–2 mm., "long." A few of the better described specific names are inserted wherever they have been associated rather definitely with any of these combinations, without regard to the correctness of this application.

Of the twelve possible combinations, it will be seen that *all* are represented: the lowest single representation being eight, the largest, seventy-five. Almost one-third of the 356 specimens are unaccounted for by the described categories.

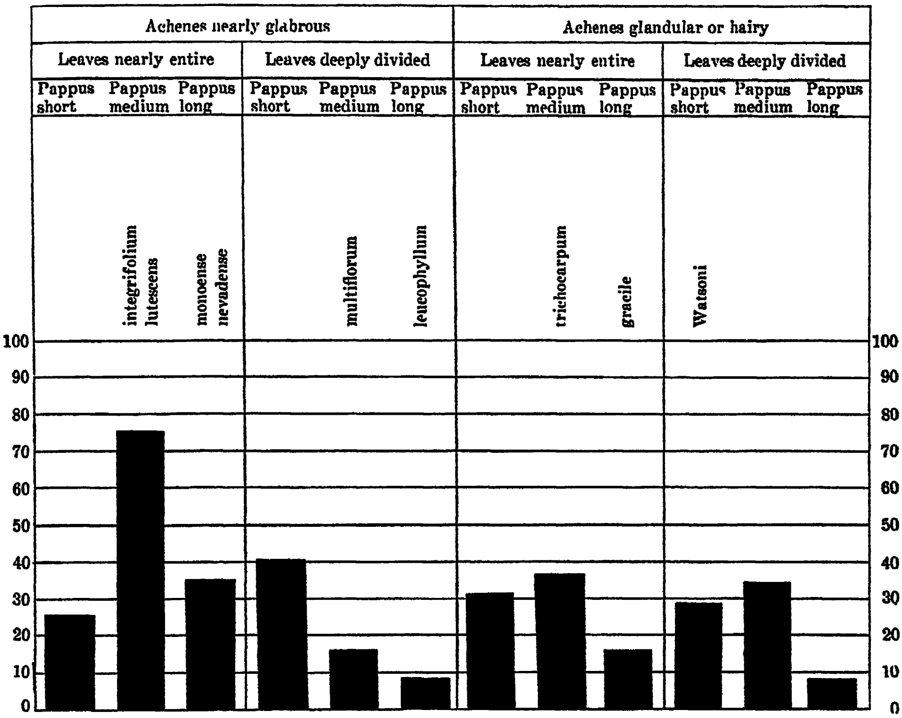

Fig. 16.—Classical segregation-criteria for var. *integrifolium.*

The writer suggests that either these should also be named, to make this classification consistent, or else that some other, more natural, criteria for delimitation must be employed.

These rigid categories break down under careful analysis. The type specimen of *Trichophyllum integrifolium* Hook. (pl. 8) does not have the achenes glabrous ("or rarely somewhat glandular-atomiferous near the summit"), as has been frequently asserted of this segregate (Gray, 1876, 1884; Greene, 1897; Howell, 1900; Coulter & Nelson, 1900). All those examined are uniformly hairy, as are those of the type specimen of *T. multiflorum* Nutt. (pl. 5) (Rydberg, 1915, 1922), the stems are somewhat branched, and the leaves are not entire, fully half of them being distinctly toothed. The original collection of *Bahia leucophylla* DC. (pl. 4) is referable to *E. lanatum* var. *typicum,* so the name is not applicable to any member of var. *integrifolium,* although it has been almost universally so employed. The pappus of the type specimen of *Bahia gracilis* Hook. & Arn. (pl. 8) (at least of those achenes examined by the writer) was medium long to distinctly short, instead of slender and much longer than the width of the achenes, as has been affirmed (Gray, 1883).

The type collections of *E. trichocarpum* Rydb. and of *E. nevadense* Gdgr. exhibit all manner of variation in achene surface, from glandular-hairy to nearly glabrous, and the frequent occurrence of such a condition in many other specimens studied suggests that this character does not possess the peculiar constancy attributed to it. To the author, it appears that the importance and stability of a few characters have been vastly overemphasized in order to accomplish a wholesale dismemberment of a large and diverse but predominantly natural population.

Without adhering too strictly to any predetermined set of characters, the individuals examined tend to group themselves about certain centers of differentiation. Thus are constituted certain minor geographical races or populations, the greater number of their members possessing certain characters in common. Within this population are to be found many which agree more closely with members of different areas, or which agree with members of none of these races. Disregarding these latter, it is perhaps of interest to note the more obvious geographical tendencies within var. *integrifolium.* That natural boundaries have not been formed between these groups may, perhaps, be owing to lack of isolation, physiological, geographical, or genetic, which would produce significant gaps in the series of intermediate plants.

The author attempts to point out the most significant structural and distributional tendencies of each group within var. *integrifolium,* without undertaking to name or delimit them. A more or less critical synonymy is given, to show the relation of the described binomials to the natural population. Whenever adequately indicated by description, range, or herbarium material, it is recorded how the principal workers have designated the forms which fell within the scope of their attention.

GEOGRAPHICAL TENDENCIES IN VAR. *INTEGRIFOLIUM*

1. Snake River plain and Middle Rocky Mts. Small slender plants, with mostly deciduous tomentum; leaves slender and entire or the larger shallowly toothed or lobed; pappus variable, but usually of medium length; achenes variously hairy to glabrous, sometimes slightly glandular.—*Trichophyllum integrifolium,* Hook., Fl. Bor. Am., 1:316. 1833; *Bahia integrifolia,* DC., Prodr., 5:656. 1836; *Eriophyllum caespitosum* var. *integrifolium,* Gray, Proc. Am. Acad., 19:26 (in part), 1883; Coulter, Man. Bot. Rocky Mt. Reg., 192. 1885; *E. integrifolium,* Greene, Fl. Franc., 444 (in part). 1897; Coulter & Nelson, New Man. Bot. Centr. Rocky Mts., 556. 1900. *Trichophyllum multiflorum,* Nutt., Jour. Acad. Phila., 7:35. 1834; *Bahia multiflora,* Nutt., Trans. Am. Philos. Soc., ser. 2, 7:373. 1841; *Eriophyllum multiflorum,* Rydb., Mem. N. Y. Bot. Gard., 1:422. 1900. *Bahia leucophylla,* T. & G., Fl. N. Am., 2:375 (in part). 1841–43; Walp., Rept. Bot. Syst., 6:175 (in part). 1846–47; Hook., Jour. Bot. Lond., 6:248. 1847; Porter, U. S. Geol. Surv. Terrs., Prelim. Rept., pt. 4, 486.

1871; Coulter, U. S. Geol. Surv. Terrs., 6^3:770. 1873; Parry, Am. Nat., 8:13. 1874.—Not *B. leucophylla* DC., 1836.

Examples: *Wyeth,* sources of Missouri (ANSP: photograph and achenes of type collection of *Trichophyllum multiflorum* Nutt.); *D. Douglas,* N(orth) W(est) C(oast of) Am(erica) (KEW: type of *T. integrifolium* Hook.); *Macbride & Payson* 2948, Hailey, Blaine Co., Ida., 1916 (CAS, P, RM, S, UC, WSC); *F. W. Peirson* 8137, south of Mammoth Hot Springs, Yellowstone, 1928 (CAS, PEIRSON); *J. A. Clark* 63, Boise, Ida., 1911 (RM, S, UC); *J. F. Macbride* 833, Squaw Cr., Boise Co., Ida., 1911 (RM, S); *Nelson & Macbride* 1432, Mackay, Custer Co., Ida., 1911 (RM, S, UC, WSC); *Maguire & Maguire* 1236, 1237, 1238, Yellowstone Nat. Park, 1932 (UC).

2. Centering in the Payette section, spreading thence to the Snake River plain (on the east), and over the Walla Walla plateau (on the northwest). Much like the preceding, with slender habit, and narrow, mostly entire leaves, but tomentum closely appressed and rather persistent; heads sometimes (but not always) larger; achenes more or less hairy, and commonly glandular; pappus variable, typically medium to long.—*Bahia gracilis,* H. & A., Bot. Beech. Voy., 333. 1838; *Eriophyllum gracile,* Gray, Proc. Am. Acad., 19:26. 1883. *E. multiflorum,* Piper, Contrib. U. S. Nat. Herb., 11:583. 1906; Frye & Rigg, Fl. NW., 406. 1912, and El. Fl. NW., 229. 1914; Piper & Beattie, Fl. SE. Wash. & Adj. Ida., 278. 1914.—Not *Trichophyllum multiflorum* Nutt., 1834.

Examples: *Tolmie* 69, Snake country (KEW: type of *Bahia gracilis* H. & A.); *Sandberg & Leiberg,* Sprague, Wash., 1893 (UC), and 183, (Ritzville, Adams Co., Wash., 1893 (CAS, O, P, UC, WSC); *J. B. Leiberg* 2255, Malheur Valley, Ore., 1896 (UC); *W. N. Suksdorf* 5090, Rockland, Wash., 1905 (P, UC, WSC); *Nelson & Macbride* 1212, Ketchum, Blaine Co., Ida., 1911 (RM, S); *J. F. Macbride* 892, Emmet, Canyon Co., Ida., 1911 (RM, S, UC, WSC); *L. F. Henderson* 8553, Vale, Malheur Co., Ore., 1927 (CAS, O); *A. R. Sweetser,* Huntington, Ore., 1905 (O).

3. Southwestern edge of the Walla Walla plateau, and through the Harney section, into the northwestern edge of the Great Basin. Plants slender, tomentum sometimes almost pannose, and usually more persistent than in foregoing; leaves slender and oblanceolate or spatulate, the larger deeply 3-cleft to somewhat pinnatifid; heads small; achenes glabrous, hairy, or even glandular; pappus variable, but usually quite short.—*Bahia leucophylla,* Eaton, *in* Wats., U. S. Geol. Expl. 40 Par., 17 (in part). 1871; *Eriophyllum caespitosum* var. *leucophyllum,* Gray, Proc. Am. Acad., 19:26 (in part). 1883; *E. leucophyllum,* Rydb., Mem. N. Y. Bot. Gard., 1:422 (in part). 1900; Howell, Fl. NW. Am., 1:355 (in part). 1900.—Not *Bahia leucophylla* DC., 1836.

This phase was included by Gray in his *Eriophyllum caespitosum* var. *leucophyllum,* and has been interpreted as *Bahia leucophylla* DC. by Rydberg, Howell, and others. The distinguishing character of *B. leucophylla,* however, was its pappus of alternately slender and short paleae, whereas the pappus is almost uniformly short in plants of the region in question. Furthermore, *B. leucophylla* is attributed to Nutka Sound (western Vancouver Island) and Mullgrave (Yakutat Bay, Alaska). Only *Eriophyllum lanatum* var. *typicum* has been collected on Vancouver Island, and no members of the genus have been reported from Alaska since the Malaspina Expedition, so far as the writer has been able to learn. The specimens upon which *Bahai leucophylla* was published are referable to *Eriophyllum lanatum* var. *typicum,* not to var. *integrifolium.*

Examples: *L. R. Abrams* 9642, Lava Butte to LaPine, Deschutes Co., Ore., 1922 (S); *M. E. Peck* 9603, LaPine, Ore., 1920 (S, WU), and 9711, Bend, Ore., 1920 (S, WU); *E. Nelson* 847, Pilot Butte, Ore., 1905 (RM, UC); *Constance* E126, Klamath Co., Ore. (CAS, O, UC), E128 (CAS, O, UC), E129 (CAS, O, RM, UC), and E131 (CAS, O, UC), Deschutes Co., Ore., 1933; *Constance & Henderson* E142 (O, UC), Deschutes Co., Ore., 1933.

4. Harney section and northern end of the Great Basin. Closely related to the preceding, but tomentum less persistent, so herbage has a dingy greenish aspect; leaves usually broader and more deeply divided; achenes pubescent and more or less glandular; pappus variable, but usually rather short.—*Bahia leucophylla,* Eaton, *in* Wats., U. S. Geol. Expl. 40 Par., 17 (in part). 1871; Anderson, Nev. Min. Bienn. Rept. 1869–70, 122. 1871; Rothr., U. S. Geol. Surv. W. 100 Par., 6:167. 1878.—Not *Bahia leucophylla* DC., 1836. *Bahia gracilis,* Gray, Bot. Calif., 1:382 (in part). 1876.—Not *B. gracilis* H. & A., 1838. *Eriophyllum Watsoni,* Gray, Proc. Am. Acad., 19:26. 1883; Blake, *in* Tidestr., Contr. U. S. Nat. Herb., 25:592. 1925. *E. trichocarpum,* Rydb., N. Am. Fl., 34:89. 1915.

Examples: *W. C. Cusick* 2605, Harney Co., Ore., 1901 (O, UC); *L. F. Henderson* 5270, Blue Mts., Grant Co., Ore., 1925 (CAS, O, S, UC), and 8554, Sawtooth Cr., Blue Mts., Harney Co., Ore., 1927 (CAS, O); *M. E. Jones,* Palisade, Nev., 1882 (CAS, P, RM, S, UC: type collection of *E. trichocarpum* Rydb.); *Constance & Henderson* E139, Klamath Co., Ore., 1933 (RM, O, UC), and E140, Lake Co., Ore., 1933 (CAS, O, RM, UC).

5. High Sierra Nevada, from Lake Tahoe to Inyo Co., Calif., and adjacent Nevada. The plants are more compact, caespitose, suffruticose at base, and densely and persistently tomentose throughout; leaves thick and spatulate, cuneate or obovate, short, entire or with 3–5 shallow lobes at apex of the larger; heads often disproportionately large; achenes nearly glabrous, or slightly hairy or glandular; pappus usually medium, but this is variable.—*Bahia integrifolia,* Gray, Bot. Calif., 1:381 (in part). 1876; *Eriophyllum caespitosum* var. *integrifolium,* Gray, Proc. Am. Acad., 19:26 (in part). 1883; *E. integrifolium,* Greene, Fl. Franc., 444 (in part). 1897; Smiley, Bot. Gaz., 59: 285. 1915; *E. lanatum* var. *integrifolium,* Smiley, Univ. Calif. Publ. Bot., 9:378. 1921.—Not *Trichophyllum integrifolium* Hook., 1833. *Bahia leucophylla,* Bolander, Enum. Pl. 1866, 11. 1867.—Not *B. leucophylla* DC., 1836. *Eriophyllum lutescens,* Rydb., N. Am. Fl., 34:87. 1915. *E. monoense,* Rydb., *l. c.; E. lanatum* var. *monoense,* Jepson, Man. Fl. Pl. Calif., 1119. 1925. *E. nevadense,* Gdgr., Bull. Soc. Bot. France, 65:40. 1918.

Examples: *W. H. Brewer* 1823, south of Mono Lake, 1863 (UC: type collection of *E. monoense* Rydb.); *Hall & Chandler* 4665, Lucile Crest, vicinity of Lake Tahoe, El Dorado Co., Calif., 8500 ft, 1903 (S, UC); *W. R. Dudley,* Yosemite Valley, 1894 (S); *H. M. Hall* 9145, Sentinel Dome, Yosemite, 8000 ft., 1911 (UC); *Constance* E109, near Lake Tahoe, Douglas Co., Nev., 1933 (CAS, O, UC); *C. F. Baker* 938, King's Canyon, Ormsby Co., Nev., 1700–2000 m., 1902 (CAS, RM, UC: type collection of *E. nevadense* Gdgr.).

The writer has shown that, using the traditional criteria, the specimens he has examined may be divided into twelve groups, seven of which have been distinguished as species by certain authors, and five hitherto unnamed. It has also been stated that, by the use of less artificial characters, at least five minor races may be designated, each of which presents a certain degree of morphological and geographical identity and coherence.

The author has, as yet, been unable to construct any arrangement which will separate this polymorphous population into natural groups without leaving a very sizable group unaccounted for. Accordingly, he considers it wise to retain the whole population in one large aggregate, *E. lanatum* var. *integrifolium*, where many of these races have been placed before by different authors. It has been sought to emphasize affinities (perhaps phylogenetic) rather than differences, to which attention has been chiefly given hitherto. Natural subdivision may, perhaps, be effected subsequently, possibly by the aid of cytological, genetic, cultural, or other experimental data, but the morphological criteria at present available seem to be insufficient for carrying this out successfully.

Specimens examined.—MONTANA. Gallatin Co.: *Payson & Payson* 1916.

WYOMING. Park Co.: *Pearson* 135, 355. Sublette Co.: *Payson & Payson* 2666, 4422. Lincoln Co.: *Payson & Armstrong* 3390; *Williams* 814. Teton Co.: *Merrill & Wilcox* 1005; *A. Nelson* 1099. Yellowstone Nat. Park: *Nelson & Nelson* 5870; *J. N. Rose* 359.

IDAHO. Fremont Co.: *Peirson* 8160; *Rydberg & Bessey* 5181. Clark Co.: *Rust* 779. Caribou Co.: *McCain* 114. Oneida Co.: *C. P. Smith* 2182. Blaine Co.: *Macbride & Payson* 2948; *Nelson & Macbride* 1212. Custer Co.: *Nelson & Macbride* 1432. Lemhi Co.: *McCain* 32. Owyhee Co.: *Nelson & Macbride* 1765. Canyon Co.: *Macbride* 892; *Mains* 7. Elmore Co.: *Evermann* 589. Ada Co.: *J. Clark* 63; Gageby (1916). Boise Co.: *Macbride* 600, 833. Washington Co.: *J. Clark* 180.

WASHINGTON. Stevens Co.: *Gabby* 31. Spokane Co.: *Piper* (1896); *Turesson* (1913). Lincoln Co.: *Sandberg & Leiberg* (1893). Chelan Co.: *St. John & Thayer* 7276; *J. W. Thompson* 5836. Kittitas Co.: *Cotton* 1139; *Whited* 493. Grant Co.: *Lake & Hull* (1892); *Piper* 3857. Adams Co.: *Sandberg & Leiberg* 183. Whitman Co.: *Elmer* 13,135; *St. John & Pickett* 6121. Walla Walla Co.: *Piper* 2425. Franklin Co.: *Hindshaw* (1896). Benton Co.: *Cotton* 405. Klickitat Co.: *Suksdorf* 5090, 11,864. Yakima Co.: *Henderson* 2292; *E. Nelson* 1482.

OREGON. Wasco Co.: *Gale* 122; *Sherwood* 15. Jefferson Co.: *Abrams* 9596; *Sweetser* (1925). Deschutes Co.: *Constance* E129; *Constance & Henderson* E142. Crook Co.: *Whited* A55, 3044. Josephine Co.: *T. Howell* 153. Klamath Co.: *Constance* E126; *Constance & Henderson* E139. Lake Co.: *Constance & Henderson* E140; *Loveless* 164. Harney Co.: *Cusick* 2605; *Henderson* 8554. Malheur Co.: *Henderson* 8555; *Leiberg* 2255. Grant Co.: *Henderson* 5270; *Peck* 16,038. Baker Co.: *Ferris & Duthie* 1055; *Sweetser* (1905). Union Co.: *Peck* 4383, 4628. Wallowa Co.: *Darlington* 288; *Gilbert* (1922).

CALIFORNIA. Modoc Co.: *M. S. Baker* (1893). Lassen Co.: *Kramer* (1932); *Robinson* 50. Plumas Co.: *Heller & Kennedy* 8687; *Mason* 1050. Sierra Co.: *Constance* E113; *Lemmon* (1874). Nevada Co.: *Constance* E111; *M. E. Jones* 2491. Placer Co.: *Blasdale* (1923); *Hawver* (1911). El Dorado Co.: *Hall & Chandler* 4665; *Pendleton & Reed* 1001. Amador Co.: *W. B. Duncan* (1927); *Hansen* 422. Alpine Co.: *Bolander* 2688; *Wolf* 5211. Mono Co.: *Brewer* 1823; *Duran* 3109. Tuolumne Co.: *Jepson* 3204; *Mason* 335. Mariposa Co.: *Dudley* (1894); *Hall* 9182. Madera Co.: *Congdon* (1895). Fresno Co.: *Hall & Chandler* 690; *Hopping* 131. Tulare Co.: *Bacigalupi* 1783. Inyo Co.: *Peirson* 1388, 8495.

NEVADA. Washoe Co.: *Heller* 10,330, 10,876. Storey Co.: *Eastwood* 14,817. Ormsby Co.: *C. F. Baker* 938; *Steinmetz* (1901). Douglas Co.: *Constance* E109; *L. S. Rose* 428. Humboldt Co.: *Greene* (1893); *Taylor & Richardson* 10. Lander Co.: *Kennedy* 4154; *Linsdale* 347. Eureka Co.: *M. E. Jones* (1882).

1*i*. Eriophyllum lanatum var. obovatum (Greene) Hall

Eriophyllum caespitosum var. *integrifolium,* Gray, Proc. Am. Acad., 19:26 (in part). 1883.—Not *Trichophyllum integrifolium* Hook., 1833.

Eriophyllum obovatum, Greene, Erythea, 3:123. 1895.

Eriophyllum lanatum var. *obovatum,* Hall, Univ. Calif. Publ. Bot., 3:86. 1907.

Eriophyllum brachylepis, Rydberg, N. Am. Fl., 34:88. 1915.

Herbage persistently white- or yellowish-tomentose. Stems few to numerous, simple, leafy, 2–3 dm. high, erect or decumbent at woody base. Leaves alternate (lowest often opposite), 1–5 cm. long, entire or coarsely few-toothed above middle; densely and equally woolly on both surfaces (tomentum sometimes closely appressed and shining); margins plane. Heads solitary, terminal. Peduncles slender or stoutish, often somewhat swollen below heads, 3–10 (or 15) cm. long. Involucres hemispheric, 7–10 mm. high, 10–12 mm. broad, of 10–12 lanceolate, acute, slightly carinate bracts; strongly overlapping and involved in copious tomentum, apparently united at base; tips usually reflexed. Rays 10–13, yellow ligules oval, 6–7 mm. long, 2.5–3 mm. wide, toothed at apex. Disk-florets 3–4 mm. long, tube glandular-hairy. Achenes 2.5–3 mm. long, cuneate-oblong, glabrous (or nearly so). Pappus of 8–10 short, obtuse, erose paleae (or some prolonged and lanceolate), 1 mm. long or less.

Range.—San Bernardino Mts., Greenhorn Range, and Lloyd Mt., southern California; 4000–7500 feet.

Although almost isolated from all other members of the species, this variety too closely approaches certain Sierran phases of *E. lanatum* to be considered distinct. Curiously enough, var. *obovatum* greatly resembles var. *lanceolatum,* endemic to the Klamath region. The two are difficult to separate, and since var. *obovatum* is inseparable from *E. lanatum,* both are here retained under that aggregate species.

Specimens with narrower leaves, longer root-crowns and thinner tomentum than ordinary, were used for the erection of *E. brachylepis* Rydb. None of the characters used for separating out this group seem to be of diagnostic value, and all possible combinations of them occur in the same area.

The following specimens represent the typical broad-leaved, conspicuously woolly phase, described as *E. obovatum* by Greene:

S. B. Parish 3716, 1895 (S, UC), *H. M. Hall* 12,895, 1899 (UC), and *W. G. Wright* 1811 (UC: type of *E. obovatum* Greene), all San Bernardino Mts., San Bernardino County.

The name, *E. brachylepis* Rydb., was published on such plants as these:

S. B. Parish 3714, 1895 (UC), and 3344, 1894 (S, UC: type collection of *E. brachylepis* Rydb.), *P. A. Munz* 10,454, 1926 (P, UC), and *F. W. Peirson* 5181, 1924 (CAS, PEIRSON), all Bear Valley, San Bernardino Mts., San Bernardino County.

W. R. Dudley 789, trail from Needles Pass to Lloyd Mt., Kern River, Tulare Co., 1895 (S), is like the San Bernardino specimens in general appearance, but has hairier achenes and longer pappus (more nearly approaching var. *lanceolatum* in the former character). *Harwood* 4320, San Bernardino Mts. (RM, P), suggests the possibility of hybridization between *E. lanatum* var. *obovatum* and *E. confertiflorum.* The intermediate characters are those of size of heads and involucres, number and form of bracts, length of peduncles, form and division of leaves, and the like.

CALIFORNIA. Tulare Co.: *Dudley* 789. Kern Co.: *Peirson* 10,688. San Bernardino Co.: *Braunton* 1032; *Parish* 3344.

1*j*. **Eriophyllum lanatum var. lanceolatum** (Howell) Jepson

Eriophyllum lanceolatum, Howell, Fl. NW. Am., 1:355. 1900.

Eriophyllum lanatum var. *lanceolatum,* Jepson, Man. Fl. Pl. Calif., 1118. 1925.

Eriophyllum Rixfordii, Eastwood, Proc. Calif. Acad., ser. 4, 20:158. 1931.

Herbage persistently white- or yellowish-tomentose. Stems several, simple, leafy, 2–4 dm. high, erect or decumbent at short woody base. Leaves alternate, thick, lanceolate to obovate, 2–4 cm. long; entire to coarsely serrate (mostly above the middle); densely and equally woolly on both surfaces; margins plane. Heads solitary to several. Peduncles stout, somewhat swollen below heads, 3–10 (or 15) cm. long. Involucres hemispheric, 8–12 mm. high, 12–15 mm. broad, of 10–15 lanceolate, acute, nearly plane bracts, strongly overlapping and involved in copious tomentum, distinct or united at base; tips reflexed. Rays 10–15, yellow ligules oblong, 7–10 mm. long, 2–3 mm. wide, toothed at apex. Disk-florets 3–4 mm. long, tube glandular-pubescent. Achenes 2–3 mm. long, cuneate-oblong, more or less hispidulous and often glandular. Pappus of 7–10 lanceolate (or oblong), acute or obtuse, erose, unequal paleae, longest 1 mm. or less.

Range.—Klamath (Siskiyou) region of Oregon (Curry, Josephine, and Jackson counties) and California (Del Norte, Humboldt, Siskiyou, and Trinity counties): 500–6500 feet.

E. lanatum var. *lanceolatum* appears to be quite distinct from any of the other varieties of the species growing in proximity to it, and has been considered a distinct species. However, it is morphologically so close to the widely removed (geographically) var. *obovatum* that it is thought best to retain both as subunits of *E. lanatum,* since var. *obovatum* approaches other varieties of that species.

Plants with the leaves conspicuously serrate, instead of nearly entire, have been described as *E. Rixfordii* Eastwood, but this foliar character is deemed insufficient to form either a specific or a varietal boundary. Such plants are represented in herbaria by the following:

H. P. Chandler 1403, Klamath River, 1901 (UC, S); *G. P. Rixford,* Shaft Rock Mt., Hilt, Calif. (CAS: type of *E. Rixfordii* Eastw.).

Several specimens have been seen which have smaller and more numerous heads, leaves predominantly entire and thinner, lower, and more slender stems, and generally less tomentose. These suggest a relationship to var. *integrifolium,* but probably belong here, as represented by:

H. M. Hall 8601 (S, UC) and 8562 (C), Salmon Mts., Trinity Co., 1909; *Alexander & Kellogg* 254, 1911 (UC), and *D. K. Kildale* 8711, Siskiyou Co., 1929 (S); *E. C. Van Dyke,* Carville, Trinity Co., 1931 (CAS).

Certain specimens from the Klamath area, which exhibit a monocephalous habit, with very much narrowed, persistently tomentose leaves (the larger of which show some traces of pinnation) and a generally reduced habit, may possibly be intermediate between vars. *lanceolatum* and *achillaeoides:*

L. R. Abrams 8637, 1922 (S), *J. W. Thompson* 4639, 1928 (S), and *D. K. Kildale* 7930, 1929 (S), all Josephine Co., Ore.; *Abrams* 8592, Del Norte Co., Calif., 1922 (S); *Kildale* 5355, Siskiyou Co., Calif., 1928 (S).

OREGON. Curry Co.: *Leach & Leach* 1563; *Peck* 4384. Josephine Co.: *Henderson & Andrews* 12,829; *Peck* 7980. Jackson Co.: *T. Howell* (1897) (O: type collection of *E. lanceolatum* Howell ?); *Peck* 16,388.

CALIFORNIA. Del Norte Co.: *Dudley* (1899); *Kildale* 8483. Humboldt Co.: *Chandler* 1403; *Tracy* 3441. Siskiyou Co.: *Alexander & Kellogg* 254; *Butler* 1394. Trinity Co.: *Hall* 8562; *Van Dyke* (1931).

2. **Eriophyllum Jepsonii** Greene

Eriophyllum Jepsonii, Greene, Pittonia, 2:165. 1891.

Shrubby perennial. Stem persistently white-pannose, 5–8 dm. high. Leaves alternate, ovate in outline, 3–6 cm. long, 1-pinnatifid into 5–7 linear, obtuse lobes; floccose on both sides, but tomentum soon deciduous above, leaving upper surface green; margins revolute. Heads loosely corymbose, at ends of erect branches. Peduncles 5–10 cm. long. Involucres broadly campanulate, 5–7 mm. high, 5–7 mm. broad, of 6–8 ovate, acute, coriaceous bracts, strongly overlapping, carinate and distinct to base. Rays 6–8, yellow ligules elliptic or oblong, 6–10 mm. long, 4–5 mm. wide. Disk-florets 3–5 mm. long, funnelform throat equalling or exceeding glandular-puberulent or -hispid tube. Style-tips obtuse. Achenes 3 mm. long, linear-clavate, 4-angled, slightly hispidulous, especially on angles. Pappus of about 8 unequal paleae, those on angles narrowly lanceolate (longest 1 mm. or less), alternating with like number of oblong, erose ones, but it would be surprising if this condition is constant.

Range.—Central Coast Ranges, California: Mt. Hamilton Range; Mt. Diablo; Arroyo Mocho (Cedar Mt.); about 1000–3000 feet.

This is a rare, narrowly endemic species, which combines many of the characters of *E. confertiflorum* and of *E. lanatum*, and perhaps constitutes an evolutionary link between the two. Some specimens of *E. confertiflorum*, those with unusually large and long-peduncled heads (*E. confertiflorum* var. *laxiflorum* Gray), approach very near to *E. Jepsonii*, and *A. D. E. Elmer* 4398, Red Mountain, Santa Clara Co., 1903 (S) is almost perfectly intermediate.

Specimens examined.—CALIFORNIA. Alameda Co.: *A. D. E. Elmer* 4646, 12 miles from Livermore, Mocho Creek, 1903 (CAS, O, S, UC), and 5030, Mocho Creek, 1903 (S, UC); *W. L. Jepson* 14,550, hills between Arroyo Mocho and Arroyo Valle, S. of Livermore, 1891 (JEPSON: type). Contra Costa Co.: *J. W. Congdon*, Mt. Diablo, 1896 (UC, JEPSON). Santa Clara Co.: *A. D. E. Elmer* 4398, Red Mt., 1903 (S).

3. **Eriophyllum confertiflorum** (DC.) Gray

Bahia confertiflora, De Candolle, Prodr., 5:657. 1836.
Bahia tenuifolia, De Candolle, *l. c.*
Bahia trifida, Nuttall, Trans. Am. Philos Soc., ser. 2, 7:374. 1841.
Bahia confertiflora var. *trifida*, Gray, Bot. Calif., 1:380. 1876.
Eriophyllum confertiflorum, Gray, Proc. Am. Acad., 19:25. 1883.
Eriophyllum confertiflorum var. *trifidum*, Gray, *l. c.*
Eriophyllum confertiflorum var. *laxiflorum*, Gray, *l. c.*
Eriophyllum confertiflorum var. *discoideum*, Greene, Man. Bot. Reg. S. F. Bay, 207. 1894.
Eriophyllum confertiflorum var. *latum*, Hall, Univ. Calif. Publ. Bot., 3:186. 1907.
Eriophyllum latilobum, Rydberg, N. Am. Fl., 34:94. 1915.
Eriophyllum trifidum, Rydberg, *l. c.*, p. 95.
Eriophyllum cheiranthoides, Rydberg, *l. c.*, p. 95.
Eriophyllum tenuifolium, Rydberg, *l. c.*, p. 96.
Eriophyllum biternatum, Rydberg, *l. c.*, p. 96.—Not *E. biternatum* (Gray) Kuntze, 1891.
Eriophyllum tridactylum, Rydberg, *l. c.*, p. 96.
Eriophyllum crucigerum, Rydberg, *l. c.*, p. 96.

Shrubby perennial, or woody only below, flowering stalks mostly herbaceous. Stem branched near base, branches slender to stout, erect, 2–6 dm. high; invested with dense, close, more or less deciduous tomentum. Leaves alternate or some opposite, 1–4 cm. long, subcoriaceous or membranaceous; cuneate to obovate in outline, 1- or 2-pinnatifid into linear divisions, or smaller leaves merely 3–5-lobed or -cleft; persistently tomentose beneath, usually glabrate and green above; margins revolute. Heads few to numerous, sessile or short-peduncled (peduncles sometimes elongated), in small terminal corymbs or heads. Involucres campanulate, tomentose, 3–5 mm. high, 3–5 mm. broad, of 4–6 broadly elliptic, obtuse, carinate bracts, strongly overlapping and distinct, or slightly united at base. Rays 4–6, sometimes wanting, yellow ligules oval or oblong, 2–4 mm. long, 1.5–3 mm. wide. Disk-florets 2–3 mm. long, puberulent to glandular-hirsute, narrowly campanulate throat exceeding short tube. Receptacle convex, foveolate. Anther-appendages ovate, obtuse. Style-tips obtuse. Achenes 2–3 mm. long, linear-clavate, 4-angled, somewhat hispidulous and often slightly glandular. Pappus of 2–14 oblong to ovate, subequal, erose paleae, 1 mm. or less in length.

Range.—Cismontane California—Coast Ranges and along the coast from Mendocino Co. to Lower California, and on the Santa Barbara, Coronados, and Cedros islands; throughout the Los Angeles Ranges, and in the Sierra Nevada foothills north to Calaveras Co.; altitudinal range from nearly sea level to 10,000 feet or more.

This is a very widespread and polymorphous species, upon the extremes of which numerous segregates have been erected. The most stable characters are the campanulate involucre of a few broadly elliptic, strongly overlapping bracts, the more or less congested inflorescence of small heads, and the semi-shrubby habit. Exceedingly variable are height and shape of plants; nature and persistence of wool; foliage; size of heads and their rays; and the length of the individual peduncles.

The typical form is the most common, that with the numerous small heads almost sessile, the leaves cuneate or broader in outline, and deeply 1- or 2-pinnatifid into narrowly linear divisions.

Constance E95, Mt. Diablo, 1933 (CAS, O, RM, UC), and E105, Jacksonville, 1933 (CAS, UC); *Epling & Ellison,* Topango Canyon, Santa Monica Mts., April, 1929 (UC, UCLA); *C. F. Baker* 778, foothills near Stanford University, 1902 (P, UC).

The most frequent departure from this state is manifested in those plants which grow in ecologically unfavorable conditions, whether from nature of the substratum, aridity, exposure, or the complex factors of high altitudinal habitat. In these the plant body is dwarfed, the leaves reduced in size, and the pination partly suppressed so that the leaves are only 3–5-cleft above the middle (sometimes nearly entire), and the heads usually less numerous. In certain mountainous districts, there seem to be indigenous races in which these characters have become genetically established. Examples of these modifications:

Constance E14, Pajaro Hills, 1933 (CAS, O, RM, UC, UCLA); *M. E. Jones* 3378, San Diego, 1882 (CAS, P, S); *Abrams & Wiggins* 236, Bletcher's Bay, Santa Rosa Is., 1931 (S, UC); *G. B. Grant* 4162, Mt. Lowe, 1904 (CAS, P, S); *T. S. Brandegee,* Cedros Is., 1897 (UC); *Hall & Babcock* 5574, basin of the Upper Kern River, 1904 (S, UC).

The other commonly divergent state is that in which the heads are distinctly peduncled (individually), sometimes very conspicuously, and often both heads and rays are larger than ordinary. Examples:

J. T. Howell 2592, Santa Ana Mts., Orange Co., 1927 (CAS, UC); *P. A. Munz* 7702, San Antonio Mts., 1923 (P, S); *G. B. Grant* 5426, Saugus, Los Angeles Co., 1903 (S, UC); *A. Eastwood* 21, Mission Hills, Santa Barbara, 1908 (UC: type collection of *E. cheiranthoides* Rydb.); *J. B. Davy* 1247, Redwood Canyon, Marin Co., 1895 (UC); *Abrams & McGregor* 311, Fort Tejon, Kern Co., 1908 (S); *J. B. Lambert,* Yosemite Valley, 1894 (S); *E. C. Van Dyke,* Idyllwild, Riverside Co., 1928 (CAS).

The former deviation, that with the reduced leaves mostly 3-lobed instead of pinnatifid, constituted Gray's *E. confertiflorum* var. *trifidum* (*Bahia trifida* Nutt., *B. confertiflora* var. *trifida* Gray, *Eriophyllum trifidum* Rydb.). The second state, characterized by the lax inflorescence, frequently accompanied by a more slender habit, was Gray's *E. confertiflorum* var. *laxiflorum* (*Bahia tenuifolia* DC., *Eriophyllum tenuifolium* Rydb.).

In addition to reviving *Bahia trifida* and *B. tenuifolia,* which had been reduced by Gray, Rydberg (1915) described five new specific segregates from *Eriophyllum confertiflorum* as here recognized. Concerning this sudden increase in the number of recognized species, Macbride (1919) writes as follows:

> It is my impression that this author has never collected in California; and the key characters which he has worked out from herbarium material and by means of which he attempts to distinguish the plants to which he has assigned names are the sort of characters that are highly variable and may be found in greater or less degree on a single specimen, a fact which should be evident, it seems to me, even from study restricted to the herbarium. The only segregate species recognized by Rydberg which I should at all hesitate to refer to one or the other of the long-established species or to one of their varieties are *E. tanacetifolium* [*tanacetiflorum*] Greene and *E. latilobum* Rydberg. . . . *E. biternatum* Rydb., *E. tridactylum* Rydb., and *E. crucigerum* Rydb., *l. c.* 96, are merely states of *E. confertiflorum* (DC.) Gray var. *trifidum* (Nutt.) Gray (*E. trifidum* (Nutt.) Rydb.), and *E. tenuifolium* (DC.) Rydb., *l. c.* 96 and *E. cheiranthoides* Rydb., *l. c.* 95, are both to be referred to *E. confertiflorum* (DC.) Gray, var. *laxiflorum* Gray.

In this concise statement, Macbride has adequately anticipated the conclusions reached, independently, by the writer concerning these proposed segregates. There is seldom any correlation between the characters drawn into service to separate these nebulous units, and different portions of the same individual will not infrequently key to different binomials.

Macbride reduced all but two of the species of Rydberg to *E. confertiflorum* vars. *trifidum* and *laxiflorum* of Gray, the first designating a type of leaf form and division, the second, a state of the inflorescence. The author had not examined many herbarium sheets before the conclusion was forced upon him that there was little correlation between these two conditions either. A list was kept of all the specimens examined, which were divided into four classes as follows:

	Heads nearly sessile	Heads conspicuously peduncled
Leaves trifid:	180	166
Leaves pinnatifid:	202	148

Thus, specimens with leaves prevailingly pinnatifid and heads closely congested, numbered 202; those with pinnatifid leaves and peduncled heads, 148; with trifid leaves and sessile heads, 180, and with trifid leaves and heads conspicuously peduncled, 166. In other words, 166 of the 696 specimens examined in this study are *both* var. *trifidum* and var. *laxiflorum* at the same time! This demonstrates clearly that these two varieties, so-called, are not actually distinct entities, but merely *states* of two different variable structures, which bear no relation to each other in their variability. For this reason the author is unwilling to retain these names or the species produced from their amplification (following in this the example of Standley (1926)).

Var. *discoideum,* of Greene, based on small plants of high altitudes from Sonoma County (near the extreme northern limit of the range of the species) was characterized by absence of rays, generally reduced habit, and large heads. A similar (genetically constant?) local race occurs in the San Antonio Mountains (near the southern limit of the range), and this has been considered identical with the more northerly phase. Such specimens as *I. M. Johnston* 1405 and 1452, San Antonio Mountains, 1917 (P, RM, S, UC), similar plants from the same area, are very interesting in this connection, in that the one exhibits well-developed rays, the other, none. Discoid individuals also occur sporadically throughout the range of the species, without any relation to the other characters (*A. King,* Arroyo Grande, San Luis Obispo Co., 1896 [UC]). In view of the wide discontinuity in range of the reduced, discoid forms, the sporadic occurrence of the eradiate condition throughout the species-population and its common occurrence in *E. lanatum* and *E. staechadifolium,* and the existence of radiate plants side by side with the discoid (with which they agree in every important character), this segregate is considered unworthy of retention.

Jepson (1925) reduced to synonymy with the species var. *latum* Hall, which was based on large plants in which the leaf divisions are unusually broad, as in these examples:

E. A. McGregor 12, Carmel Valley, 1906 (S); *S. B. & W. F. Parish,* San Bernardino, 1888 (UC); *A. D. E. Elmer* 4564, Black Mt., Santa Clara Co., 1903 (O, S, UC); *A. Eastwood* 8949, San Gabriel Canyon, 1919 (CAS); *E. L. Koethen* 20, plains, Riverside, 1897 (UC: type of *E. confertiflorum* var. *latum* Hall). As the cited material illustrates, this leaf-state is of sporadic occurrence, and is probably without taxonomic value.

Specimens examined.—CALIFORNIA. Mendocino Co.: *Eastwood* (1926); *Ferguson* 75. Sonoma Co.: *M. S. Baker* 3169a; *Tidestrom* (1895). Solano Co.: *Brandegee* (Suisun). Marin Co.: *Constance* E13; *Davy* 1246. Contra Costa Co.: *Bowerman* 2225; *Constance* E95. Alameda Co.: *Constance* E102; *J. T. Howell* 1621. San Francisco Co.: *Jepson* 10,583. San Mateo Co.: *Davy* 772; *L. S. Rose* 33,176. Santa Clara Co.: *C. F. Baker* 5048; *Elmer* 4564. Santa Cruz Co.: *Mexia* (1926); *C. A. Reed* (1916). Monterey Co.: *Constance* E23; *Heller* 6752. San Benito Co.: *Abrams & Borthwick* 7830; *Eastwood* 6963. San Luis Obispo Co.: *Brewer* 457; *Eastwood* 13,773. Santa Barbara Co.: *Eastwood* 21; *Ewan* 5325. Anacapa Is.: *J. T. Howell* 3797. San Miguel Is.: *Hoffmann* (1930). Santa Cruz Is.: *Abrams & Wiggins* 214; *Wolf* 2810. Santa Rosa Is.: *Abrams & Wiggins* 236; *Dunn* (1931). Ventura Co.: *Hall* 6589; *Mason* 515. Los Angeles Co.: *G. B. Grant* 4162; *Munz* 6093. San Clemente Is.: *Abrams & Wiggins* 341; *Munz* 6710. Santa Catalina Is.: *Dunkle* 1800; *Millspaugh* 4486. San Bernardino Co.: *Jepson* 5525; *Parish* 5823. Orange Co.: *Abrams* 1834; *J. T. Howell* 2592. Riverside Co.: *Ewan* 3084; *Munz* 5857. San Diego Co.: *Eastwood* 9092; *Spencer* 1066. Imperial Co.: *McGregor* 982. Calaveras Co.: *Davy* 1487; *Stanford* 395. Tuolumne Co.: *Constance* E105; *A. L. Grant* 67A. Mariposa Co.: *H. Edwards* (1871) (UC: fragment and photo of type of *E. tridactylum* Rydb.); *Hall & Hall* 9089. Madera Co.: *Eastwood* 12,554; *Tompkins* (1894). Fresno Co.: *A. L. Grant* 1140; *J. McDonald* (1915). Inyo Co.: *Brandegee* (1913). Tulare Co.: *C. F. Baker* (*Culbertson*) 4452 (UC: type collection and type fragment of *E. biternatum* Rydb.); *Hall & Babcock* 5574. Kern Co.: *Abrams & McGregor* 311; *Heller* 7774.

LOWER CALIFORNIA. Mainland: *Mearns* 3497; *Munz* 9569. Cedros Is.: *Greene* (1885); *Palmer* 700 (CAS: type collection of *E. crucigerum* Rydb.). Coronados Is.: *Greene* (W. Am. Scientist, 1:70. 1885).

E. confertiflorum has been attributed to Arizona, but the author has been unable to discover any definite record of the occurrence or collection of the species there.

3*a*. **Eriophyllum confertiflorum var. tanacetiflorum** (Greene) Jepson

Eriophyllum tanacetiflorum,* Greene, Pittonia, 2:21. 1889.

Eriophyllum confertiflorum var. *tanacetiflorum*, Jepson, Man. Fl. Pl. Calif., 1116. 1925.

Shrubby throughout (or erect, nearly simple branches somewhat herbaceous), 3–6 cm. high, clothed with close pannose tomentum, sometimes persistent, sometimes deciduous. Leaves alternate (or some opposite), thin or membranaceous, 2–5 cm. long; spatulate to obovate in outline, deeply 3–5 lobed or pinnatifid; oblong divisions entire or toothed; white-tomentose or -floccose beneath, glabrate above; margins revolute. Heads 3–10, almost sessile (or some peduncles 2.5 cm. long or less) in terminal corymbiform clusters. Involucres campanulate, 5–7 mm. high, 5–6 mm. broad, tomentose, of 5–7 ovate, acute or obtuse, strongly overlapping, carinate bracts, distinct or slightly united at base. Rays 4–6 (frequently wanting), yellow ligules oval or oblong, 4–5 mm. long, 3 mm. wide. Disk-florets 3.5–4 mm. long, narrowly campanulate throat exceeding tube; both more or less glandular-hairy. Achenes 3.5 mm. long, linear-clavate, 4-angled, sparingly appressed-pubescent to nearly glabrous. Pappus of about 8 unequal, narrowly oblong, obtuse, erose paleae, longest about 1 mm.

Range.—Sierra Nevada foothills, 1000–3000 feet, in Calaveras and Mariposa counties, California.

The characters of this variety are little (if at all) beyond the limits of variation of the species, and are, in the main, only distinctions of size and number of structures. However, when one removes from var. *tanacetiflorum* the various anomalous forms added by Rydberg (1915), it forms a fairly coherent geographical division of *E. confertiflorum*. The rather shrubbier habit; larger heads; more numerous bracts; and larger leaves, ligules, disk-florets, and achenes, serve to distinguish it from at least the average of the species. It would hardly be possible to construct a key which would separate properly all plants of the two. It is on the basis of this correlation of unusually large size and more numerous parts, with geographical coherence, that this is retained in varietal status.

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* The specific name given this by Greene was *tanacetiflorum*, not "tanacetifolium," as it is usually erroneously written.

Specimens examined.—CALIFORNIA. Calaveras Co.: *F. E. Blaisdell,* Mokelumne Hill (CAS); *J. B. Davy* 1513, limestone ridge, Murphy's Camp, 1895 (UC); *E. L. Greene,* Calaveras Co., 1889 (UC). Mariposa Co.: *J. W. Congdon,* Split Rock Ferry trail, 1893 (UC), new Coulterville road, 1896 (UC), and new Coulterville road, 1897 (S, UC); *C. B. Wolf* 4862 and 5118, above Merced River, NW of Bagby, on Coulterville road, Upper Sonoran zone, 1500 ft., 1933 (RSA).

PLANTS POSSIBLY OF HYBRID ORIGIN

? E. confertiflorum × *lanatum* var. *arachnoideum.*—Rydberg's *E. latilobum* is based upon the single collection: *A. A. Heller* 8584, back of San Mateo, on the Half Moon Bay road, San Mateo County, 1907 (GRAY: type, S). This is an exceedingly puzzling plant, which the writer believes may be of hybrid origin (although no genetic nor cytological evidence is yet available to support this contention), the possible parents being *E. lanatum* var. *arachnoideum* and *E. confertiflorum.* The arguments for this view are summarized in the following table:

Eriophyllum lanatum var. *arachnoideum*	*Eriophyllum latilobum*	*Eriophyllum confertiflorum*
Leaves broad and thin, rhombic in outline, with broadly cuneate entire base, deeply 3–5-lobed at middle or above; lobes sinuately dentate, glabrate above; 2–5 cm. long.	Leaves broad and thin, rhombic to obovate in outline, with oblong or cuneate entire base; deeply 3-cleft at middle or above, the broadly oblong-lanceolate lobes often toothed or lobed, especially above middle; loosely floccose below, glabrate above, 2–6 cm.	Leaves membranaceous, cuneate to obovate in outline, with a narrow winged or wingless petiole; deeply pinnatifid or 3–5-cleft at middle or above; lobes linear, white-tomentose beneath, more or less glabrate above; 1–4 cm. long.
Heads large (2 cm. or more in breadth), solitary; peduncles 3–7 cm. long.	Heads intermediate (8–10 mm. broad), few (10 or less), in lax corymbs, peduncles 0.5–8 cm. long.	Heads small (5–6 mm.), sessile or on very short peduncles, numerous in terminal corymbose clusters.
Involucres hemispheric, 9–11 mm. high, 15 mm. broad, of 8–15, oblong-ovate, acute, weakly overlapping bracts.	Involucres broadly campanulate, 4–5 mm. high, 7–10 mm. broad, of 6–8 ovate, acute, weakly overlapping bracts.	Involucres campanulate, 3–5 mm. high, 3–5 mm. broad, of 4–6 broadly elliptic, obtuse, strongly overlapping bracts.
Achenes turbinate, glabrous, striate, muriculate, 3–4 mm. long.	Achenes turbinate, striate, muriculate, glabrous (or some with a few hairs on angles), 3 mm. long.	Achenes clavate-linear, sparingly hispidulous and more or less glandular, 2–3 mm. long.

From this summary, it may be seen that the leaf characters are prevailingly those of *E. lanatum* var. *arachnoideum,* while their division suggests *E. confertiflorum;* heads and involucres are intermediate; achenes are primarily those of the first, but the modified shape, size, and the occasional presence of a few hairs on the angles point to the second; other structures are all referable to one or the other of the possible parent-species, or else manifest an intermediate nature. The writer believes that he has given sufficient data to justify the suggestion that *E. latilobum* Rydb. = *E. confertiflorum* × *E. lanatum* var. *arachnoideum*. This opinion is further borne out by the additional facts that all three occur in this same region, and that all achenes of Rydberg's type specimen examined by the writer proved to be empty and sterile.

The specimen, *A. D. E. Elmer* 4397, San Mateo, San Mateo Co., 1903 (CAS, O, P, S, UC), also has sterile achenes, and may be from the same colony as the last. The leaves are pinnately incised, the divisions much narrower, and more or less deeply toothed or lobed.

? *E. confertiflorum* × *lanatum* var. *obovatum*.—The specimen, *Harwood* 4320, San Bernardino Mts. (P, W), upon similar evidence, appears to be of hybrid origin, also. The parent stocks, both growing together in this region, may be *E. confertiflorum* and *E. lanatum* var. *obovatum*.

4. **Eriophyllum staechadifolium** Lagasca

Eriophyllum staechadifolium, Lagasca, Gen. et Sp., 28. 1816.
Helenium staechadifolium, Sprengel, Syst., 3:574. 1825.
Bahia artemisiaefolia, Lessing, Linnaea, 5:160. 1830; and *l. c.*, 6:253. 1831.
Bahia staechadifolia, De Candolle, Prodr., 5:656. 1836.
Bahia staechadifolia var. *Californica*, De Candolle, *l. c.*, p. 656.
Bahia artemisiaefolia var. *Douglasii*, De Candolle, *l. c.*, p. 657.
Eriophyllum staechadifolium var. *depressum*, Greene, Bull. Calif. Acad., No. 2:404. 1887.
Eriophyllum artemisiaefolium, O. Kuntze, Rev. Gen., 336. 1891.
Eriophyllum staechadifolium var. *artemisiaefolium*, Macbride, Contr. Gray Herb., 59: 39. 1919.

Shrubby perennial, much-branched stem 3–15 dm. high, covered with close, tardily deciduous tomentum. Leaves alternate (or some opposite), subcoriaceous, 3–7 cm. long, lanceolate to ovate in outline; 1- or 2-pinnatifid into narrowly oblong, mostly obtuse divisions; or uppermost leaves, or majority of them on dwarfed plants, often linear-oblong, entire or few-toothed or -lobed; all persistently white-tomentose below, but soon green and glabrate (or nearly so) above; margins revolute. Heads numerous, short-peduncled, in dense but loose corymbiform panicle. Involucres campanulate, 4–5 mm. high, 2–3 mm. broad, of 8–11 oblong, obtuse or acute, carinate bracts, little overlapping and distinct to base. Rays 6–9 (sometimes wanting), yellow ligules elliptic, entire or toothed at apex, 3–5 mm. long, 2–3 mm. wide. Disk-florets 4 mm. long, glandular, narrowly campanulate throat exceeding tube. Receptacle convex, foveolate. Anther-appendages ovate, obtuse. Style-tips obtuse. Achenes 3–4 mm. long, linear-oblong, 4-angled, more or less hispidulous and glandular. Pappus of 8–12 unequal, oblong or oblanceolate, obtuse, erose paleae, those on angles usually longer (1 mm. or more).

Range.—Near the coast, from Bandon (Coos Co.), Oregon, to Gaviota (Santa Barbara Co.), California, and Santa Cruz, Anacapa, and Santa Rosa islands (California); from sea level to 200 or 300 feet.

This species is fairly constant in reproductive characters, but variable in habit and foliage. A series of geographical tendencies in foliar characters is exhibited throughout the range, so that, by these, it is possible to determine rather accurately from what locality a given specimen has been obtained. These local forms intergrade so gradually, however (two or more types often appearing on the same individual), that it seems inadvisable to attempt to segregate them, especially as other characters remain stable. Most of the several segregates proposed owe their origin to this diversity in foliar aspect.

The type of *E. staechadifolium* Lag. was presumably collected at Monterey, whence plants seem to have a higher percentage of narrow, entire leaves than those from elsewhere. This is considered here as the most striking of the diverse leaf-types, but of no more significance than the many others of less conspicuous form. The following herbarium material represents this foliar phase:

Constance E24, Pacific Grove, 1933 (CAS, O, RM, UC, UCLA); *A. A. Heller* 6704 (in part), Pacific Grove, 1903 (RM, S, UC); *Patterson & Wiltz,* cliffs near Pacific Grove, 1907 (C, RSA, S).

The phase designated *Bahia artemisiaefolia* by Lessing (collected at San Francisco by Chamisso) has broader, more pinnatifid leaves, the other characters being essentially equivalent to those of the last. This is exemplified by:

C. Dudley, Pacific Grove, 1926 (CAS); *Ewan, Grant, & Ballon* 7920, Surf, 1933 (UCLA, EWAN); *A. A. Heller* 5695, Cliff House, San Francisco, 1902 (P, RM, S); *J. P. Tracy* 4971, Cape Mendocino, 1918 (CAS, P, UC); *I. L. Wiggins* 3793, Pescadero Beach, 1929 (S, UC).

While extremes of the two phases are strikingly dissimilar, they are, in the opinion of the writer, too intimately connected by a host of intermediate forms to justify their continuance under separate names. The author has seen no plants, save stunted ones (even at the type locality), with *all* the leaves entire, the larger ones being more or less lobed or divided in all healthy individuals. The uppermost leaves or most of the leaves on dwarfed specimens are likely to be reduced and entire, or nearly so, on plants throughout the range of the species. It appears to be impossible to delimit these two leaf-types without bisecting a number of individual plants. The following herbarium sheets manifest both types of foliage on the same specimen:

A. Eastwood 4751, Pt. Reyes, 1915 (CAS); *A. D. E. Elmer* 4833, Watsonville, 1903 (CAS, O, P, S, UC); *E. L. Greene,* Goat Is., 1882 (S); *W. L. Jepson* 14,542, Monterey, 1896 (UC, JEPSON); *G. Newell,* Pacific Grove (CAS); *Mrs. C. H. Thompson,* Coast, Del Mar, 1902 (S).

Greene's var. *depressum,* based on dwarfed specimens collected on Santa Cruz Island, has rather broad, thick leaves, the pinnation of which is partly suppressed. Although the specimens seen are rather striking, the habital and foliar characters are scarcely sufficient to distinguish them from similarly reduced plants of the neighboring mainland, and the inflorescence offers no additional characters. Examples:

J. T. Howell 3798, Anacapa Is., 1928 (CAS), and 6364, Prisoner's Harbor, Santa Cruz Is., 1931 (CAS); *A. Swain,* Santa Cruz Is., 1919 (CAS); *C. B. Wolf* 2901, between Orizaba & Baby's Cove, 200 feet, Santa Cruz Is., 1933 (RSA).

Bahia staechadifolia var. *Californica* DC. appears to have been described from stunted plants, with most of the leaves narrow and entire, the heads fewer than normal, and the involucres conspicuously tomentose; *B. artemisiaefolia* var. *Douglasii* DC., from plants with larger heads and ligules than usual and more densely tomentose habit (possibly juvenile specimens). These variations are of little significance and both names have long since lapsed into synonymy with *Eriophyllum staechadifolium.*

Especially in the northern part of the range of the species, it is not unusual to find plants with discoid heads growing with the normal radiate, as:

L. F. Henderson 10,010, mouth of Pistol River, Curry Co., Ore., 1929 (O, UC); *J. P. Tracy* 3108, 5 mi. south of Crescent City, Del Norte Co., Calif., 1909 (UC), and 4361, Patrick's Point, Humboldt Co., Calif., 1913 (UC).

Since this condition also occurs sporadically in *E. lanatum* and *E. confertiflorum,* it is not to be considered of taxonomic import here.

Specimens examined.—OREGON. Coos Co.: *Peck* 8990. Curry Co.: *Henderson* 11,412; *Peck* 8427.

CALIFORNIA. Del Norte Co.: *Jepson* 9045; *Tracy* 3108. Humboldt Co.: *Heller* 13,878; *Tracy* 4971. Mendocino Co.: *M. E. Jones* 29,113; *Wolf* 1318. Sonoma Co.: *Eastwood* 4879; *J. T. Howell* 5280. Marin Co.: *Constance* E20; *Mason* 1153. Contra Costa Co.: *Hall* 1650; *McMinn* 139. San Francisco Co.: *C. F. Baker* 5049; *Heller* 5695. San Mateo Co.: *C. F. Baker* 1747; *Wiggins* 3793. Santa Cruz Co.: *Elmer* 4833; *C. H. Thompson* (1902). Monterey Co.: *Constance* E24; *Heller* 6704. San Luis Obispo Co.: *Eastwood* 14,950; *Peirson* 2235. Santa Barbara Co.: *Munz* 11,379; *Peirson* 8256. Anacapa Is.: *J. T. Howell* 3798. Santa Cruz Is.: *J. T. Howell* 6364; *Wolf* 2901. Santa Rosa Is.: *Brandegee* (Proc. Calif. Acad. Sci., ser. 2, 1:213. 1888; and Zoe, 1:139. 1890); *Yates* (State Min. Rept. 1889, 184. 1890).

5. Eriophyllum Nevinii Gray

Eriophyllum Nevinii, Gray, Syn. Fl., ed. 2, 1^2:452. 1886.

Shrubby perennial, tomentum deciduous from stems in age. Stem branching, thick, ascending, 3–10 dm. high. Leaves alternate, broadly ovate in outline, 8–20 cm. long, 1- or 2-pinnatifid into numerous oblong, obtuse lobes, equally white-tomentose on both sides; margins revolute. Heads numerous in naked, flat-topped, compound cymes, individual peduncles 1 cm. or less. Involucres campanulate. tomentose, 6–7 mm. high, 5–6 mm. broad, of 8–12 oblong, obtuse, carinate bracts, little overlapping and distinct to base. Rays 6–8, inconspicuous and little surpassing disk, yellow ligules elliptic, 2 mm. long, 1 mm. wide, obscurely toothed at apex. Disk-florets 3–4 mm. long, narrowly campanulate throat exceeding glandular-pubescent tube. Receptacle low-convex, naked. Anther-appendages narrowly ovate. Style-tips obtuse. Achenes 3–4 mm. long, linear-clavate, 4-angled, hispidulous on angles. Pappus of 3–6 unequal entire or erose paleae, longer slender and lanceolate, 1.5 mm. or less.

Range.—Rocky bluffs along the coast, San Clemente and Santa Catalina islands, Calif.

E. Nevinii is a beautifully distinct and constant, exclusively insular species, although it is obviously related to *E. staechadifolium.* Millspaugh and Nuttall (1923) speak of "a form with finely divided leaves and blunter bracts," from "cliffs near Sugar Loaf," Santa Catalina Island, which the writer has not seen, but these variations would seem to be of very minor importance.

Specimens examined.—CALIFORNIA. Los Angeles Co.: San Clemente Is.: *Abrams & Wiggins* 378; *Peirson* 3477. Santa Catalina Is.: *Jepson* 3050; *Wolf* 4249.

6. **Eriophyllum nubigenum** Greene

Eriophyllum nubigenum, Greene, *in* Gray, Proc. Am. Acad., 19:25. 1883.
Actinolepis nubigena, Greene, Fl. Franc., 442. 1897.

Annual, herbage densely and permanently white-tomentose. Stem branched from base and above, leafy branches erect, 5–15 cm. high. Leaves alternate, narrowly spatulate or oblanceolate, entire or obscurely toothed, 1–2 cm. long. Heads solitary, terminal. Peduncles 1 cm. long or less. Involucres narrowly campanulate, 5–6 mm. high, 3–4 mm. broad, of 4–6 bracts, oblong, acute, carinate, and distinct to base. Rays 4–6, yellow ligules elliptic, inconspicuous and scarcely exceeding disk, about 1 mm. in length. Disk-florets few (about 10), 2 mm. long, campanulate throat exceeding the somewhat glandular-hairy tube. Receptacle conical. Anther-appendages ovate, obtuse. Style-tips obtuse. Achenes 2.5–3 mm. long, linear, 4-angled, pubescent with long, soft white hairs. Pappus of 8–10 oblong, obtuse, erose, subequal paleae, 0.5–1.5 mm. long.

Range.—A rare plant from the Yosemite (Mariposa Co., Calif.); 5000–9000 ft.

It is very possible that this interesting endemic species has been overlooked by collectors because of its striking resemblance to one or more of the Inuleae, the rays here being inconspicuous and the whole plant densely white-woolly.

Specimens examined.—CALIFORNIA. Mariposa Co.: *K. Curran,* Cloud's Rest, Yosemite, 1883 (S: cotype of *E. nubigenum* Greene); *Mrs. Dodd,* Yosemite, 1891 (UC: cotype of *E. nubigenum* Greene); *J. W. Congdon,* Chilnualna Falls, 1897 (S), and Chilnualna trail, 1897 (S).

6*a*. **Eriophyllum nubigenum var. Congdoni** (Brandegee) n. comb.

Eriophyllum Congdoni, Brandegee, Bot. Gaz., 27:449. 1899.

Loosely floccose annual, tomentum probably deciduous with age. Stem erect or ascending, freely branched from base to middle, 1–3 m. high. Leaves alternate, spatulate to oblanceolate, entire or the larger toothed at apex, 1–3 cm. long. Heads solitary, terminal. Peduncles 3–10 cm. long. Involucres campanulate, 5–8 mm. high, 5–6 mm. broad, of 8–10 oblong, acute, carinate bracts, distinct to base. Rays 6–10, elliptic ligules yellow, 3–5 mm. long, 2 mm. broad, obscurely dentate at apex. Disk-florets about 20, 2–3 mm. long, funnelform throat exceeding the glabrous to somewhat glandular-hairy tube. Receptacle convex, obtuse. Anther-appendages ovate, obtuse. Style-tips obtuse. Achenes 2.5–3 mm. long, linear, 4-angled, pubescent with long, soft, white hairs. Pappus of 6–10 unequal, alternately obtuse oblong, and acute lanceolate, erose paleae, 1–2 mm. long.

Range.—Also a rarity from the Sierra Nevada, Mariposa Co.; about 1500–3000 ft.

Specimens examined.—CALIFORNIA. Mariposa Co.: *J. B. Lambert,* mountains near Henessey's, 1894 (UC: type of *E. Congdoni* Brandegee); *H. M. Hall* 8848, Merced Canyon, Upper Sonoran zone, 2000 ft.; 1911 (S, UC, W, JEPSON).

The species and the variety present a very interesting problem in determination of specific delimitations. The variety differs from the species chiefly in the following respects: less woolly habit; larger leaves, peduncles, heads, involucres, rays, and disk-florets; more numerous involucral bracts, ligules, and disk-florets; the pappus, of alternating lanceolate acute and oblong obtuse paleae; and altitudinal range. The two agree in form of leaves, involucres, receptacle, anther-appendages, and style-tips; in shape, size, and peculiar pubescence of achenes; and in geographical range, both being known only from the same part of the same mountain range, although at slightly different altitudes.

This disparity in habitat elevation may account for much of the difference in degree of wooliness, and in size and number of certain structures. In the writer's opinion, the variety is the normal state of the plant, while the type of the species is a dwarfed alpine representative of it. The only character that seems to oppose such a treatment is the difference in the aspect of the pappus. Unfortunately, no complete series of specimens, from altitudes of from 2000 to 9000 feet, has been collected, but only extreme types. In view of the inadequacy of material, the author does not feel himself justified in reducing *E. Congdoni* to synonymy with *E. nubigenum,* but retains the former in varietal status, with the suggestion that more extensive collection may, perhaps, furnish a basis for further reduction.

7. **Eriophyllum ambiguum** Gray

Bahia Wallacei, Gray, Proc. Boston Soc. Nat. Hist., 7:146. 1859.—Not *B. Wallacei* Gray, 1857.
Lasthenia (Monolopia) ambigua, Gray, Proc. Am. Acad., 6:547. 1865.
Bahia parviflora, Gray, Bot. Calif., 1:382. 1876.
Bahia ambigua, Gray, *l. c.*
Eriophyllum ambiguum, Gray, Proc. Am. Acad., 19:26. 1883.
Eriophyllum paleaceum, Brandegee, Bot. Gaz., 27:450. 1899.
Eriophyllum parviflorum, Rydberg, N. Am. Fl., 34:86. 1915.
Eriophyllum Parishii, Hall: Constance, Madroño, 2:114. 1934, as a synonym.

Floccose, annual, thin wool tardily deciduous from stem and leaves. Stem branched at base, erect, ascending or diffuse, 0.5–3 dm. high. Leaves alternate, spatulate to narrowly oblanceolate, entire or the broader with few teeth or lobes toward apex, 0.5–4 cm. long. Heads solitary, terminal. Peduncles 1–8 cm. long. Involucres campanulate, 3–8 mm. high, 3–7 mm. broad, of 6–9 oblong-lanceolate, rigid, carinate bracts, either distinct or loosely united to two-thirds their length. Rays 5–10, oval or oblong ligules yellow, 2–10 mm. long, 2–3 mm. wide, toothed at apex. Disk-florets 2–3 mm. long, broadly funnelform throat exceeding the short, glandular-hispid tube. Receptacle narrowly conical, naked or somewhat chaffy near apex, with linear scales. Anther-appendages narrowly ovate, obtuse or acute. Style-tips short-conical. Achenes 2.5 mm. long, linear, prismatic, more or less pubescent, or the inner quite glabrous. Pappus a crown of 6–9 obtuse, erose, hyaline scales, 0.3 mm. long or less, or entirely obsolete.

Range.—Western rim of the Sonoran Desert (Mohave division) and adjacent ranges (Inyo and Kern, to San Bernardino and Riverside cos., Calif.); 500–7500 ft.

Concerning the numerous segregates made from this species Hall (1907) says:

> It would not be difficult to segregate a number of species from the aggregate *E. ambiguum* if one had only the ertreme forms. An abundance of material shows, however, that species based on length and number of rays, union or separation of involucral bracts, character of pappus, and presence or absence of chaff on the receptacle, are neither natural nor of scientific value. Not only do these characters vary greatly, but they may be found in almost all possible combinations, the variations not being concomitant.

The studies of the writer have confirmed this view, and the synonyms listed above are regarded as minor sporadic variants in this, the most polymorphous of the annual species.

The named segregates may be treated conveniently in the following four groups:

(*a*) Involucral bracts distinct; rays hardly longer than disk; receptacle scrobiculate.—*Bahia parviflora* Gray; *Eriophyllum parviflorum* Rydb. Examples: *J. T. Howell* 5043, Kern Canyon, 2770 ft, 1930 (CAS).

(*b*) Involucral bracts distinct; rays conspicuous; receptacle chaffy.—*Eriophyllum paleaceum* Brandegee. Examples: *T. S. Brandegee,* Kernville, 1892 (UC: cotype of *E. paleaceum* Brandegee), Olanche, 1891 (UC: cotype of *E. paleaceum* Brandegee); *Hall & Chandler* 7092, Argus Mts., 5700 ft., 1906 (UC); *J. T. Howell* 5019, near Walker Pass, 1930 (CAS); *C. A. Purpus* 5358, Walker Pass, 1897 (UC); (and, with bracts of receptacle fewer and smaller:) *T. S. Brandegee,* Kernville, 1891 (UC); *Hall & Chandler* 6873, near Johannesberg, Mohave Desert, 1906 (P, RM, UC), and 6941, Pleasant Canyon, Panamint Mts., 7500 ft., 1906 (UC).

(*c*) Involucral bracts distinct; rays conspicuous; receptacle nearly or quite smooth.—*E. Parishii* Hall *ex* Constance. Examples: *H. M. Hall* 5760, Palm Springs, Colorado Desert, 1905 (O, P, RM, S, UC); *S. B. Parish* 6088, Colorado Desert, 1907 (O, UC).

(*d*) Involucral bracts united; rays conspicuous; receptacle nearly naked.—*Lasthenia* (*Monolopia*) *ambigua* Gray; *Bahia ambigua* Gray; *Eriophyllum ambiguum* Gray. Examples: *J. T. Howell* 5143, Glenville, Greenhorn Range, 3200 ft.; 1930 (CAS); *H. M. Hall* 6297, Fort Tejon, 1905 (UC); *Dr. Van Horn,* Fort Tejon, 1864 (UC: fragment of type of *Bahia ambigua* Gray).

This species is of particular interest in that it appears partly to bridge the gap between the annual species of *Eriophyllum* and section *Pseudobahia* Gray of *Monolopia* DC. (Constance, 1934).

Specimens examined.—CALIFORNIA. Inyo Co.: *Ferris, Scott, & Bacigalupi* 3959; *Hall & Chandler* 6941. Kern Co.: *Hall* 6297; *Hall & Babcock* 5030. San Bernardino Co.: *Hall & Chandler* 6856; *Munz & Keck* 7877. Riverside Co.: *Hall* 5760; *Parish* 6088.

? ARIZONA. Mohave Co.: *Lemmon & wife* (1884).

8. Eriophyllum lanosum Gray

Burrielia (*Dichaeta*) *lanosa,* Gray, Pac. R. R. Rept., 4:107. 1857.
Actinolepis lanosa, Gray, Proc. Am. Acad., 9:198. 1874.
Eriophyllum lanosum, Gray, Proc. Am. Acad., 19:25. 1883.
Antheropeas lanosum, Rydberg, N. Am. Fl., 34:98. 1915.
Antheropeas tenuifolium, Rydberg, *l. c.,* p. 99.

Floccose annual, stems sparingly branched, ascending or erect, slender, 3–15 cm. high. Leaves alternate, linear to narrowly oblanceolate, entire (or occasionally lobed toward apex), 0.5–2 cm. long. Heads solitary, terminal. Peduncles 1–5 cm. long. Involucres campanulate, 5–6 mm. high, 3–7 mm. broad, of 8–10 linear-oblong, acute, carinate bracts, distinct or nearly so. Rays 5–10, oval or oblong ligules white or rose-tinged, toothed at apex, 2–5 mm. long, 1–3 mm. wide. Disk-florets 2–3 mm. long, funnelform throat little exceeding glandular-puberulent tube. Receptacle convex, obtuse, naked. Anther-appendages linear-subulate. Style-tips obtusely conical, or cuspidate. Achenes 2–2.5 mm. long, linear, sparingly pubescent. Pappus of 4–6 hyaline, lanceolate palea, produced into slender awns, alternating with equal number of oblong, obtuse ones, about ½ as long, longest 1–2 mm.

Range.—Sonoran desert and Mexican highland, of the Basin and Range province, and Lower California province (southern California, from San Bernardino Co., south to Lower California, and east, through southern Arizona and Nevada, to southern Utah); 500–3500 feet.

This is a rather rare plant in California, but is not uncommonly collected in Arizona. The specific characters are fairly stable, except for variation in ray-color, and in length of pappus. A specimen with the two types of pappus-squamellae subequal—*T. S. Brandegee,* San Sebastian, Lower California, 1889 (UC: type collection)—was the basis for *Antheropeas tenuifolium* Rydb. The value of this segregate, based upon a single character, is extremely doubtful. *Eriophyllum lanosum* is intimately related to the following species, *E. Wallacei.*

Specimens examined.—CALIFORNIA. Kern Co.: *Lemmon* (1884). San Bernardino Co.: *Ferris* 7241; *Munz & Harwood* 3606. San Diego Co.: *Jepson* 8571.

ARIZONA. Mohave Co.: *Eastwood* 18,133; *M. E. Jones* 3874. Yavapai Co.: *M. E. Jones* (1903). Yuma Co.: *Newlon* 572. Maricopa Co.: *Gillespie* 8937; *Palmer* 604. Pinal Co.: *Abrams* 12,941; *Eastwood* (1919). Pima Co.: *Ewan* 5372; *Thornber* 384. Greenlee Co.: *Davidson* (So. Calif. Acad., Bull., No. 6: 35. 1907). Cochise Co.: *Pringle* (1881).

NEVADA. Lincoln Co.: *Goodding* 2207; *M. E. Jones* 5036W. Clark Co.: *M. E. Jones* (1894), (1904).

UTAH. Washington Co.: *Goodding* (1902); *M. E. Jones* (1880).

LOWER CALIFORNIA. *Brandegee* (1889–Rancho Viejo); *Palmer* 782.

9. Eriophyllum Wallacei Gray

Bahia Wallacei, Gray, Pac. R. R. Rept., 4:105. 1857.
Bahia rubella Gray, Bot. Mex. Bound., 95. 1859.
Actinolepis Wallacei, Gray, Proc. Am. Acad., 9:198. 1874.
Actinolepis Wallacei var. *rubella,* Gray, *l. c.*
Eriophyllum Wallacei, Gray, Proc. Am. Acad., 19:25. 1883.
Eriophyllum Wallacei var. *rubella,* Gray, *l. c.*
Eriophyllum aureum, Brandegee, Bot. Gaz., 27:449. 1899.
Antheropeas Wallacei, Rydberg, N. Am. Fl., 34:98. 1915.
Antheropeas rubellum, Rydberg, *l. c.*
Antheropeas australe, Rydberg, *l. c.*
Eriophyllum Wallacei var. *calvescens,* Blake, Jour. Wash. Acad., 19:278. 1929.

Annual, densely and persistently white-tomentose throughout. Stem branched at base, erect, ascending or decumbent, 2–15 cm. high. Leaves alternate, linear-spatulate to obovate, entire or the larger 3-lobed at apex, 8–20 mm. long. Heads solitary, terminal. Peduncles 1–3 cm. long. Involucres campanulate, 5–7 mm. high, 5–6 mm. broad, of 5–10 ovate, carinate bracts, distinct or nearly so. Rays 5–10, oval ligules usually yellow, but occasionally turning white, or not rarely rose- or purple-tinged, or white, entire or toothed at apex, 3–4 mm. long, 2–3 mm. wide. Disk-florets 2–3 mm. long, funnelform throat little exceeding glandular-pubescent tube. Receptacle low-conical, obtuse, naked. Anther-appendages linear-subulate. Style-tips conical, acute. Achenes 2 mm. long, linear, obtusely angled, glabrous to more or less hairy. Pappus of 6–10 oval or oblong, obtuse, erose, opaque white paleae, less than 1 mm. long, or reduced to a mere crown, or obsolete.

Range.—Sonoran desert (including the Mohave division), Salton trough, and Mexican highland, of the Basin and Range province, adjoining ranges, and onto the Colorado plateau (Inyo and Kern counties, Calif., south to Lower California, west to Los Angeles Co., and eastward, through southern Nevada and Arizona, to southern Utah); 1000–5000 ft.

This is a relatively constant species for this unstable genus, but it exhibits sporadic minor variations in length of pappus, color of ligules, and pubescence of achenes, which have been employed for the setting up of specific and varietal segregates of no geographical significance and of little natural or scientific value.

Individuals with rays colored other than yellow, differing constantly in no other respect from the normal yellow-rayed plants, have received the designations: *Bahia rubella* Gray; *Actinolepis Wallacei* var. *rubella Gray; Eriophyllum Wallacei* var. *rubella* Gray; *Antheropeas rubellum* Rydb. Examples:

T. S. Brandegee, Mason's, Colorado Desert, 1896 (UC); *P. A. Munz* 9699, Laguna Mts., 1925 (P, S, UC).

In examining herbarium material, the writer found little correlation between ray color and entire or toothed ligules, and so follows Hall (1907) in considering this a sporadic color-form.

The names, *Eriophyllum aureum* Brandegee and *E. Wallacei* var. *calvescens* Blake, are founded on specimens like the normal, except that the pappus is reduced to a crown or is obsolete. Both of these, again, are segregates based upon a single character, notoriously variable throughout the genus. They represent no geographical entities, and so are not retained by the writer. Examples:

L. R. Abrams 11,865, Red Rock Canyon, Kern Co., 1927 (P, S); *T. S. Brandegee,* Lone Pine, 1891 (UC: type of *E. aureum* Brandegee); *Greata* 572 (in part), Redlands, 1906 (RM, UC); *R. Hoffmann,* Redman to Muroc, 1929 (CAS).

A specimen with conspicuous pappus and hairy achenes has been designated *Antheropeas australe* Rydb., but these two variations are not concomitant, so the segregate appears to be worthless. Examples:

H. M. Hall 2053, Chalk Hill, San Jacinto Mts., 1901 (UC); *C. R. Orcutt,* mountains, N. Lower California, 1884 (UC: fragment of type of *Antheropeas australe* Rydb.).

Specimens examined.—California. Inyo Co.: *Bailey & Robison* (1930); *Heller* 8240. Kern Co.: *Abrams* 11,800; *J. T. Howell* 4979. San Bernardino Co.: *Hall & Chandler* 6757; *Jepson* 15,484. Los Angeles Co.: *Ewan* 3280; *Moxley* 893. Riverside Co.: *Hall* 6012; *Jepson* 12,597. San Diego Co.: *Munz* 9699; *Peirson* 5935. Imperial Co.: *Ferris* 7062.

Nevada. Clark Co.: *M. E. Jones* 5036Y, 5045q.

Arizona. Mohave Co.: *Eastwood* 18,122a; *Wilson* 1893. Yavapai Co.: *M. E. Jones* (1903); *Palmer* 224.

Utah. Washington Co.: *Goodding* 819; *M. E. Jones* 1631.

Wyoming. Albany Co.: *E. Nelson* 4336a. *Coulter & Nelson* (New Man. Centr. Rocky Mts., 556. 1900).

Lower California. *Greene* (1885); *Peirson* 5843.

10. **Eriophyllum multicaule** (DC.) Gray

Actinolepis multicaulis, De Candolle, Prodr., 5:656. 1836.
Actinolepis multicaulis var. *papposa*, Gray, Proc. Am. Acad., 6:546. 1865.
Eriophyllum multicaule, Gray, Proc. Am. Acad., 19:24. 1883.

Floccose annual, tomentum deciduous except from heads. Stem branched at base, decumbent, ascending or diffuse, 2–15 cm. high. Leaves cuneate or spatulate, usually obtusely toothed or lobed at apex, 1 cm. long or less. Heads nearly sessile, in small leafy-bracteate clusters at ends of branches. Involucres campanulate, 3–4 mm. high, 3 mm. broad, of 5–7 elliptic, strongly boat-shaped, distinct bracts. Rays 3–7, obovate ligules yellow, 2 mm. long, 1 mm. wide. Disk-florets 2 mm. long or less, campanulate throat little exceeding pubescent tube. Receptacle nearly flat. Anther-appendages ovate, obtuse. Style-tips obtuse. Achenes 2 mm. long, linear, angled, pubescent to glabrous. Pappus of 10–15 slender, hyaline, acuminate, unequal paleae, fimbriate into short marginal bristles, terminal longest, or pappus obsolete in abortive achenes.

Range.—California Coast Ranges and Los Angeles Ranges, of the Pacific Border province, and reappearing in central Arizona, in the Basin and Range province (cismontane California, from Monterey to San Diego Co., and Yavapai Co., Ariz., but apparently not collected in the intervening area); from near sea level to 2000 feet.

The type collection was a plant with all (or most) of the disk-florets sterile, their styles nearly entire, achenes glabrate and abortive, and pappus obsolete. Normal plants with pappus of disk-florets like that in rays were the basis of Gray's name, *Actinolepis multicaulis* var. *papposa*, a varietal distinction which he (1874) reduced to synonymy with the species.

Specimens examined.—CALIFORNIA. Monterey Co.: *Bacigalupi* 1151; *Jepson* 15,913. San Benito Co.: *J. T. Howell* 6006; *Mason* 6921. San Luis Obispo Co.: *Eastwood* 15,105; *Ferris* 7617. Santa Barbara Co.: *Brewer* 404; *Jepson* 11947. San Bernardino Co.: *Johnston* 1373; *Parish* 5590. Riverside Co.: *Jepson & Hall* 1272; *Peirson* 2927. San Diego Co.: *M. E. Jones* (1882).

ARIZONA. Yavapai Co.: *Jared* (1892); *Palmer* 221.

11. **Eriophyllum Pringlei** Gray

Eriophyllum Pringlei, Gray, Proc. Am. Acad., 19:25. 1883.
Actinolepis Pringlei, Greene, Fl. Franc., 441. 1897.

Loosely and copiously woolly annual, tomentum persistent or tardily deciduous below. Stems diffusely branched, 1–5 cm. high, forming dense tufts. Leaves spatulate, 3-lobed at apex, 1 cm. or less in length. Heads nearly sessile in small leafy-bracteate clusters at ends of branches. Involucres campanulate, 6 mm. high, 5 mm. broad, of 6–8 elliptic, strongly boat-shaped, distinct bracts. Rays wanting. Disk-florets 2.5 mm. long, campanulate throat usually exceeded by glandular tube. Receptacle nearly flat. Anther-appendages ovate, obtuse. Style-tips obtuse. Achenes 2 mm. long, linear, angled, appressed-pubescent. Pappus of 5–10 silvery-scarious, oblong-lanceolate, obtuse paleae, fimbriate into several marginal bristles, about 2 mm. long, usually equaling corolla.

Range.—Sonoran desert (including Mohave division) of the Basin and Range province, and bordering mountains (Mono and Inyo cos., south to San Diego Co., west to Ventura and Los Angeles cos., Calif., and east to southern Arizona); 3000–6000 ft.

The specimens examined exhibit no significant variations, and no segregates of this species have been described. *E. Pringlei* is closely related to the preceding species, *E. multicaule*.

Specimens examined.—California. Mono Co.: *Shockley* 372. Inyo Co.: *Hall & Chandler* 7194; *Heller* 8241. Kern Co.: *Hall & Babcock* 5075; *Peirson* 7826. San Bernardino Co.: *Davy* 2281; *Jepson* 6127. Ventura Co.: *Abrams & McGregor* 229; *Epling & Wheeler* 1791. Los Angeles Co.: *J. T. Howell* 4876; *Mason* 2997. Riverside Co.: *Hall* 1542. San Diego Co.: *Jepson* 8732; *M. E. Jones* (1906–Banner).

Arizona. Mohave Co.: *M. E. Jones* 3888 (1903). Yavapai Co.: *M. E. Jones* (1903–Congress Jct.), (1903–Hillside). Maricopa Co.: *M. E. Jones* (1903); *Peebles, Harrison, & Kearney* 5104. Gila Co.: *Eastwood* 17,134. Pima Co.: *Peebles & Harrison* 1195. Cochise Co.: *Parish* 115.

SPECIES EXCLUDED

1. *Eriophyllum absinthifolium,* Kuntze, Rev. Gen., 336. 1891. = Bahia absinthifolia Bentham.
2. *Eriophyllum alternifolium,* Kuntze, *l. c.*, p. 336. = Bahia alternifolia Lessing.
3. *Eriophyllum ambrosioides,* Kuntze, *l. c.*, p. 336. = Bahia ambrosioides Lagasca.
4. *Eriophyllum anthemoides,* Kuntze, *l. c.*, p. 336. = Achyropappus anthemoides Gray.
5. *Eriophyllum bahiaefolium,* Greene, Fl. Franc., 446. 1897. = Monolopia bahiaefolia Bentham. (Constance, 1934.)
6. *Eriophyllum Bigelovii,* Kuntze, *l. c.*, p. 337. = Bahia Bigelovii Gray.
7. *Eriophyllum biternatum,* Kuntze, *l. c.*, p. 337. = Bahia biternata Gray.
8. *Eriophyllum chrysanthemoides,* Kuntze, *l. c.*, p. 337. = Bahia dissecta (Gray) Britton.
9. *Eriophyllum Heermannii,* Greene, *l. c.*, p. 445. = Monolopia Heermannii Durand. (Constance, 1934.)
10. *Eriophyllum minus,* Rydberg, N. Am. Fl., 34:86. 1915. = Monolopia minor De Candolle. (Constance, 1934.)
11. *Eriophyllum mohavense,* Jepson, Man. Fl. Pl. Calif., 1117. 1925. = Eremonanus mohavensis Johnston.
12. *Eriophyllum neomexicanum,* Kuntze, *l. c.*, p. 337. = Achyropappus neomexicanus (Gray) Rydberg.
13. *Eriophyllum nudicaule,* Kuntze, *l. c.*, p. 337. = Bahia nudicaulis Gray.
14. *Eriophyllum oblongifolium,* Kuntze, *l. c.*, p. 337. = Bahia oblongifolia Gray.
15. *Eriophyllum oppositifolium,* Heynhold, Nom. Bot. Hort., 1:310. 1840. =Bahia oppositifolia Nuttall.
16. *Eriophyllum pedatum,* Kuntze, *l. c.*, p. 337. = Bahia pedata Gray.
17. *Eriophyllum resinosum,* Kuntze, *l. c.*, p. 337. = ? Galinsoga resinosa De Candolle.
18. *Eriophyllum sinuata,* Kuntze, *l. c.*, p. 337. = Loxothysanus sinuatus (Lessing) Robinson.
19. *Eriophyllum Woodhousii,* Kuntze, *l. c.*, p. 337. = Bahia Woodhousii Gray.

Transmitted May 23, 1934.

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EXPLANATION OF PLATES

PLATE 3

Eriophyllum caespitosum Douglas. Plants grown in the gardens of the Horticultural Society of London, from seed transmitted by *Douglas,* from Northwest America. Specimens at the Royal Botanic Gardens, Kew.

PLATE 4

Bahia leucophylla De Candolle. Part of the type collection, *Neè et Haenke,* at the Conservatoire Botanique de la Ville de Genève.

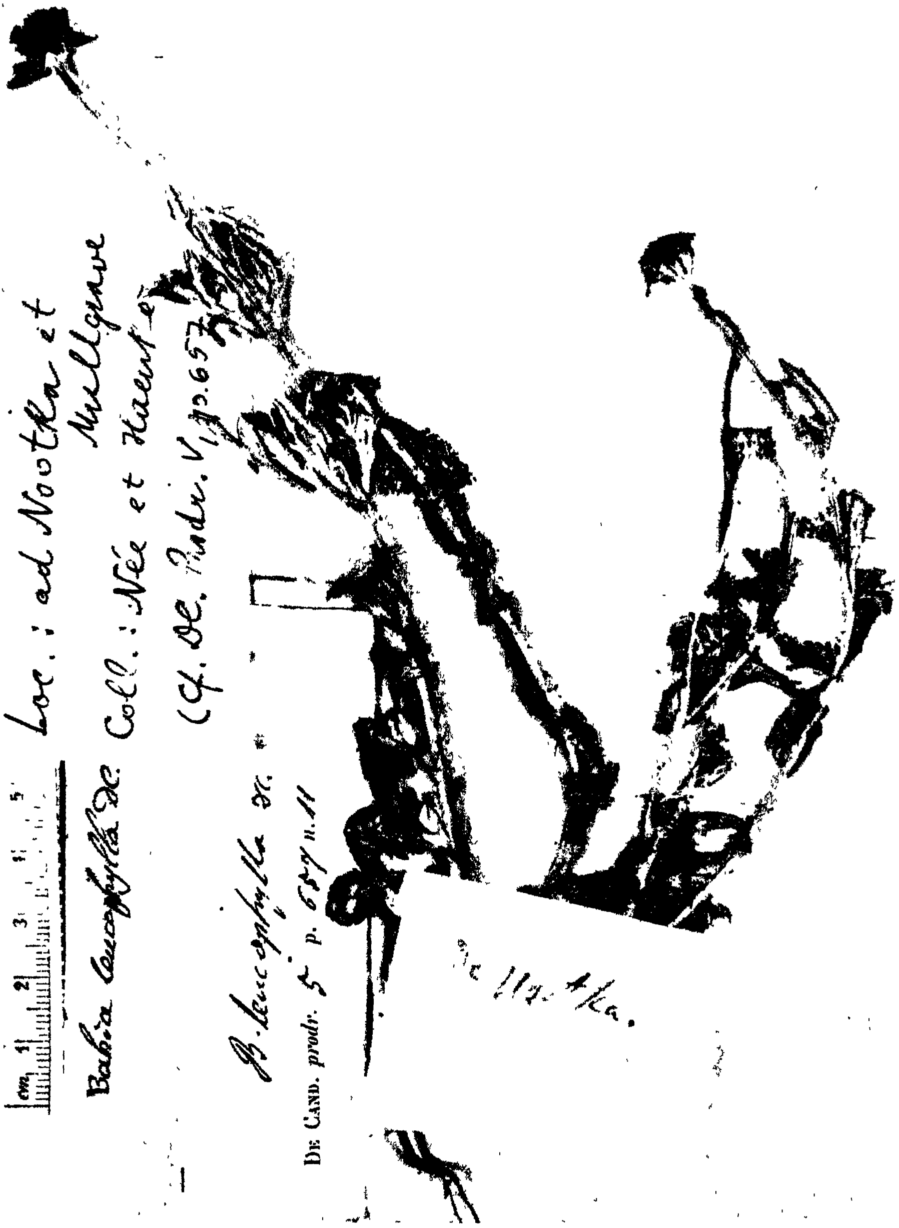

cm 1 2 3 4 5
Babia leucophylla DC.
Loc.: ad Nootka et Mullgrave
Coll.: Née et Haenke
(Cf. DC. Prodr. V, p. 657)
B. leucophylla DC.
De Cand. prodr. 5 p. 657 n. 11
de Nootka.

PLATE 5

Eriophyllum lanatum (Pursh) Forbes var. *Hallii* Constance. The type specimen, *Hall* 6272, in the University of California Herbarium, Berkeley.

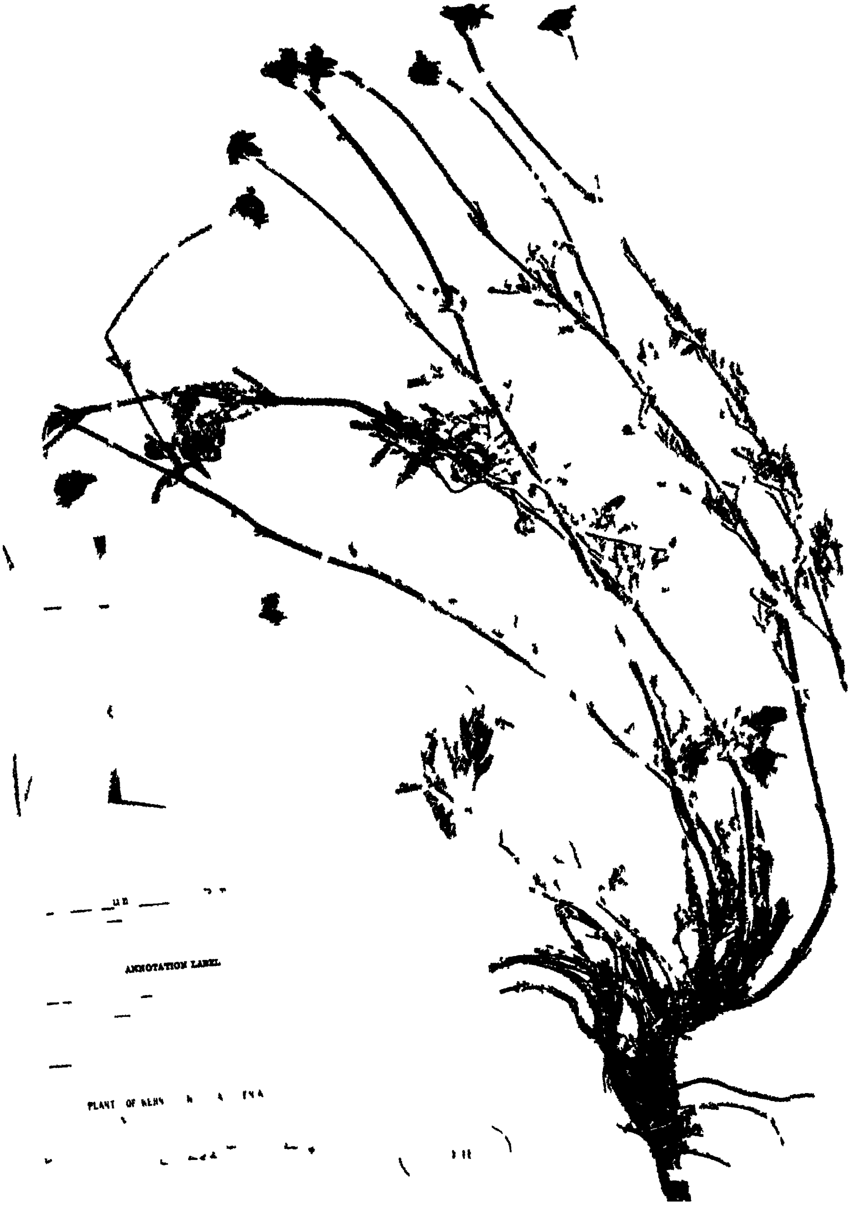

ANNOTATION LABEL
PLANT OF NEHS

PLATE 6

Trichophyllum integrifolium Hooker. The type specimen, *Douglas*, at the Royal Botanic Gardens, Kew.

PLATE 7

Trichophyllum multiflorum Nuttall. The type collection, *Wyeth*, at the Academy of Natural Sciences, Philadelphia.

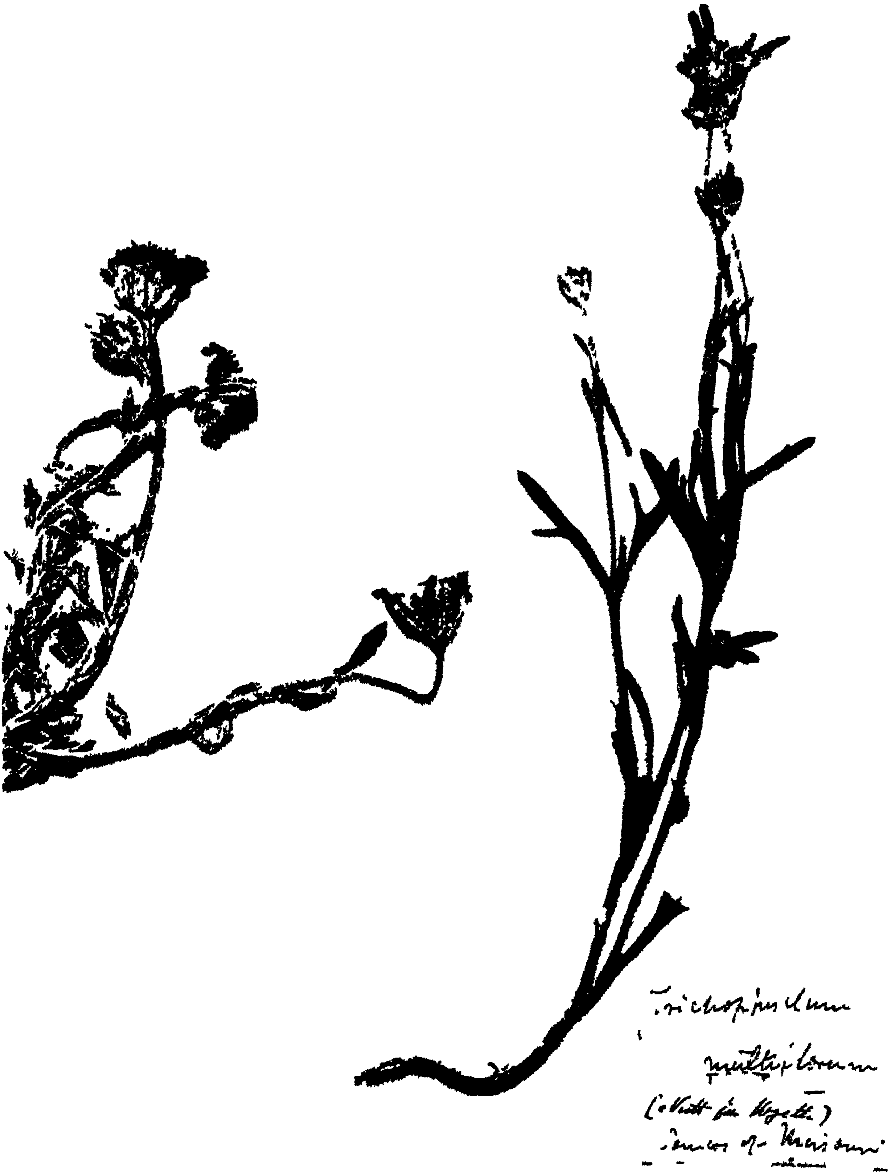
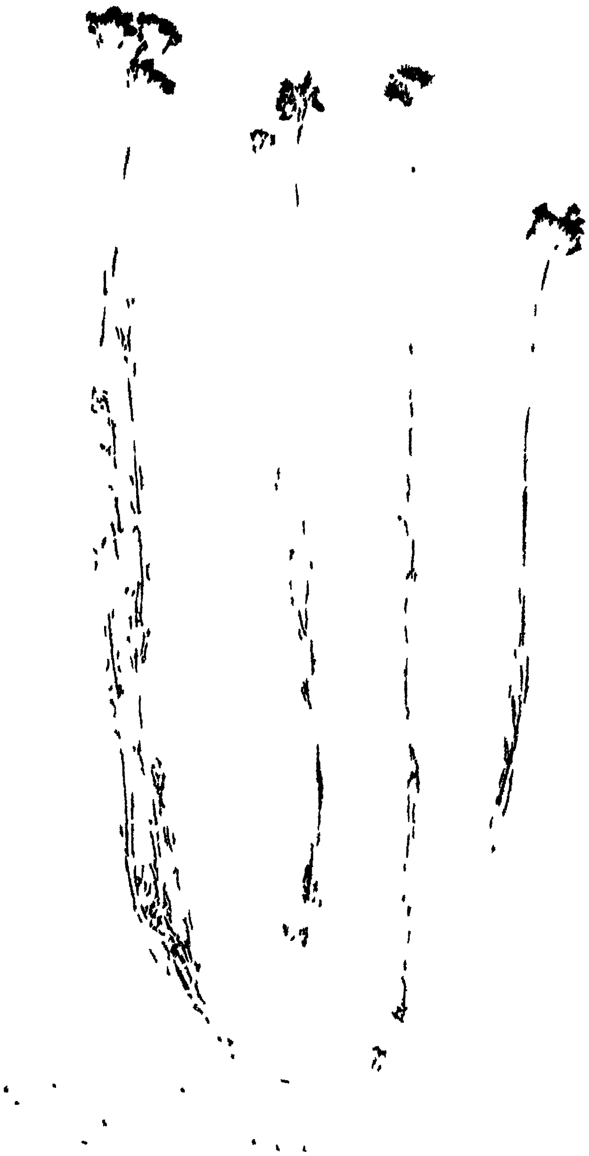

Trichophyllum
multiflorum
(Nutt. fide Engelm.)
Sources of Missouri

PLATE 8

Bahia gracilis Hooker & Arnott. The type specimen, *Tolmie* 69, at the Royal Botanic Gardens, Kew.



THREE NEW SPECIES OF NICOTIANA FROM PERU

BY

T. H. GOODSPEED

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THREE NEW SPECIES OF NICOTIANA FROM PERU

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DURING 1935–1936 the University of California Botanical Garden maintained an expedition in South America under the author's direction. Its primary objective concerned determination of the limits of natural variation and distribution of the species of the genus *Nicotiana* described from temperate South America. Members of the expedition collected in Peru, Bolivia, Chile, and Argentina. The new or little known species of *Nicotiana* which were found will be described in a series of reports, the present one* having to do with material from the Peruvian collections.

Nicotiana Benavidesii sp. nov.

Nicotiana viscosa; foliis profunde cordatis; inflorescentiis columnari-paniculiformibus; calycibus brevidentibus; corollis late tubularibus, dilute viridiflavescentibus; stigmatibus antherisque conspicue exsertibus.

Type.—University of California Botanical Garden Expedition to the Andes, 1935–1936, 3797 (U. C. Herbarium 548750, 548751). Coll. James West, Nov. 8, 1935, 3 km. from bridge on trail from Pachachacas Bridge to Abancay, Dept. Apurimac, Peru. Alt. 2200 m. "Lining road, on gentle, dry slope and waste ground. Height of plant +3 m. 'Ccamasayu.'" *Other authentic material:* University of California Botanical Garden Expedition to the Andes, 1935–1936, 3848 (U. C. Herbarium 548727, 548728). Coll. James West, Nov. 11, 1935, Rio Limatambo, near confluence with Apurimac, Dept. Cuzco, Peru. Alt. 2300 m. "Gravelly flats. Height of plant 2–3 m." Field Museum Herbarium 900032 and 900037, and University of California Herbarium 583630, 583631, and 583632. Coll. C. Vargas C., Universidad del Cuzco Museo de Historia Natural, Sección Botánica, 328, May, 1937. Hda. "Sisal," quebrada de Marcahuasi, Prov. Anta, Dept. Cuzco, Peru. Alt. 2400 m. "Semiarbustiva."

Large, sparsely branched, soft-woody shrub 2–3 m. high. Stem to 3 cm. in diameter, younger portions fleshy, densely puberulent, moderately viscid, older parts more woody, thinly covered with shallowly fissured cork, branches assurgent-erect, their leafy apices distinctly flat topped unless terminated by inflorescences. Leaves large, strictly petiolate; petiole viscid puberulent, commonly half as long as blade, near inflorescence much shorter; blade to 30 cm. long, 32 cm. wide, rotund-cordate or elliptic-cordate, apex retuse, base with lobes prolonged inwards, these extensions overlapping or ± erect, main veins evident, both surfaces pubescent, lower surface viscid. Inflorescence columnar, a long, pubescent main axis and numerous short, branched, pubescent, floriferous laterals; pedicels commonly as long as calyx, flowers pendent, odorless. Calyx poculiform, 8–10 mm. long, 6–7 mm. wide, densely puberulent, ± viscid, light canescent green, colorless intersepal tissue almost lacking, teeth short, triangular. Corolla tube 35–45 mm. long, about 10 mm. wide, broadly clavate-cylindric with additional short, slight dilation immediately below the somewhat contracted mouth, glabrous, commonly glossy, within calyx white, above

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pale greenish yellow; limb short (4–5 mm.), faintly 5-lobed, plicate in bud, prior to anther dehiscence ascendent, then often horizontal or reflexed, dull pale greenish yellow, upper surface glabrous, lower surface sparsely puberulent. Filaments pale greenish, inserted on corolla at apex of ovary, densely lanuginose for several mm. above insertion, then glabrous, generally of three lengths, none appreciably longer than corolla tube when flower opens, by anther dehiscence all exserted 5–15 mm.; anthers light green, elliptic, medifixed. Pollen straw-colored. Hypogynous disk pale orange. Ovary green, conical; style pale green, slightly shorter than longest stamens; stigma thick discoid, shallowly sulcate. Capsule rotund-oval, acute, 10–15 mm. long, commonly exserted, walls slightly woody, outer surface reddish brown, on dehiscence valves bifid. Seeds numerous, dull brown, angular, ca. 0.6 mm. long, less in width, surface shallowly reticulate, meshes small, irregular, ± lobed, frequently rather narrow; embryo straight. Chromosome number 12 pairs.

Allied to *N. Raimondii* Macbr. and *N. solanifolia* Walp., possibly also to *N. glutinosa* L. From the first two readily distinguished by exserted stamens and retuse leaf apex, from *N. glutinosa* by columnar paniculiform inflorescence and tubular corolla.

Grown in the University of California Botanical Garden,* the stem of *N. Benavidesii* showed cork formation as early as the first autumn. Like *N. Raimondii,* flowering did not begin until late the first year and thereafter appears to be more or less continuous. There is no suggestion of red in the flowers, although they readily discolor to brownish red on drying.

With his permission, *N. Benavidesii* is named in honor of General O. R. Benavides, President of the Republic of Peru, whose government in many ways assisted the University of California Botanical Garden Expedition to the Andes throughout its work in Peru.

Nicotiana thyrsiflora sp. nov.

Nicotiana pubescens, frutescens; foliis caulinis confertis, oblanceolatis; inflorescentiis longis, anguste cylindricis, dense floriferis; corollis brevibus, tubularibus, virido-flavescentibus.

Type.—A. Weberbauer 7015. Coll. July 6, 1914, between Huamachuco and Angasmarca, Prov. Santiago de Chuco, Dept. Libertad, Peru. Alt. 3800–3900 m. "Spärlich verzweigter Strauch, bis 3 m. hoch, Bl. grünlich gelb. Mit Gras und Sträuchen bewachsene, kleine steinige Schluchten, auch an Felsblöcken in der Grassteppe." (Berlin, Gray, Field Museum.) Annotation on sheet "Nicotiana thyrsiflora Bitter," but never published. *Other authentic material:* University of California Botanical Garden Expedition to the Andes, 1935–1936, 8179 (U. C. Herbarium 583633–583641 inc.) Coll. James West, Dec. 1, 1936, about 2 km. S. of Tres Cruces Pass, on trail Huamachuco–Angasmarca, Prov. Santiago de Chuco, Dept. Libertad, Peru. Alt. about 3800 m. "Height of plant 1.75 m. Flower more or less horizontal in position, bright, slightly greenish yellow."

Sparingly branched shrub 2–3 m. high. Stem thick, densely puberulent, internodes very short. Leaves all 15–20 cm. long, 2–3.5 cm. wide, sessile or tapering-subpetiolate, narrowly oblanceolate, plane to markedly undulate, often much twisted, both surfaces densely puberulent, apex acute or subacute, margin entire, frequently revolute, lateral veins numerous, regularly spaced slender ribs. Inflorescences narrow, densely floriferous cylinders at least 50 cm. long, 5–8 cm. wide, central axis about 1 cm. in diameter, laterals approximate, very short (1–7 cm.), suberect, monochasially branched, subtended by ligulate-lanceolate bracts 30–80 mm. long, 5 mm. wide, and furnished with smaller lanceolate bracts 10–20 mm. long, 2–3 cm. wide; pedicels 10–13 mm. long; flowers usually ± horizontal. Calyx poculiform, 12–16 mm. long, 9–10 mm. wide, pubescent, teeth broadly triangular, unequal, 2–3 mm. long, colorless intersepal tissue inconspicuous or lacking. Corolla greenish yellow, glabrous or nearly so; tube 16 mm. long, 9 mm. wide, broadly obconic-cylindric; limb spreading, short (4–5 mm.), scalloped into 5 very shallow, broadly obtuse, sometimes mucronulate lobes. Stamens inserted on corolla tube about 5 mm. above base; filaments woolly in lower part, glabrous above; anthers broadly elliptic, medifixed, included. Hypogynous disk prominent. Ovary broadly oval; style rather thick; stigma pulvinate, sulcate, slightly above anthers, at mouth of corolla tube or a little exserted. Capsule broadly oval, about 12–15 mm. long. Seeds dull brown, oblong-ovoid, nearly 1 mm. long, surface shallowly reticulate, meshes small, ridges slightly wavy, embryo straight or nearly so.

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* Assistance under a Works Progress Administration project is acknowledged.

This rather unique species has not yet been grown in the University of California Botanical Garden. According to Mr. West, who collected and photographed it in northern Peru, the habit of the plant is strikingly suggestive of *Digitalis purpurea.* The yellow greenish flower closely approximates that of *N. rustica,* but the leaf is predominantly sessile, a character never before found in the species group to which *N. rustica* belongs. It is possible that *N. thyrsiflora* may prove to be of amphidiploid origin.

Nicotiana Knightiana sp. nov.

Nicotiana subpulverulento-pubescens; foliis petiolatis, cordatis, rotundo-cordatis aut ellipticis; inflorescentiis paniculiformibus; corollarum tubis brevibus, sericeo-dealbatis, dilute viridibus et limbis crenatis, obscure-viridibus.

Type.—University of California Botanical Garden Expedition to the Andes, 1935–1936, 04161 (U. C. Herbarium 548735, 548736, 548737). Coll. Ynes Mexia, Nov. 16, 1935, near Mollendo, Prov. Islay, Dept. Arequipa, Peru. Alt. about 40 m. "Hills near ocean, near a trickle of water. A small colony in partially cultivated land. 'Tabaquilla.' "

Erect, leafy annual or limited perennial to 2 m. high, in age forming rather dense bush 1.5 m. in diameter. Stem to 2–3 cm. in diameter, ridged, subpulverulent-canescent, branches alternate, assurgent. Leaves strictly petiolate, petiole occasionally approaching but not equaling length of blade; blade to about 30 cm. in both length and width, cordate, rotund-ovate, or elliptic, base equal or unequal, apex obtuse, margin repand or undulate, main veins evident, both surfaces pubescent, upper surface slightly pulverulent, lower whitish, felted-pulverulent with adpressed, interwoven, unbranched, tapering, sigmoid filamentous hairs. Inflorescences 50–75 cm. long, complexly determinate, simulating somewhat narrow, decompound panicles with long, pubescent main axis and numerous short, wiry, pubescent or viscid pubescent branches; lowermost bracts foliaceous, petiole rather short, blade ovate or lanceolate, apex obtuse or acute, all other bracts very small, subulate, deciduous; pedicels shorter than calyx, later about equaling capsule; flowers usually horizontal or slightly declinate, odorless. Calyx poculiform, 9 mm. long, 5 mm. wide, light green, pulverulent-pubescent, sometimes viscid, colorless intersepal tissue reduced to narrow wedges, teeth short, broadly triangular. Corolla tube 25 mm. long, broadly clavate, 3–4 mm. wide within calyx, increasing to 6 mm. in width above calyx, immediately below mouth becoming abruptly dilated to 7 mm., at mouth contracted to 5 mm., actually pale yellow green, but conspicuously dealbate with short sericeous hairs; limb short (3–4 mm.), plicate in bud, ascendent on first expanding, thereafter commonly ± horizontal, faintly notched into 5 broadly obtuse, almost truncate, frequently mucronulate lobes, dark green (near Ridgway's "empire green") marked with lighter green at rim and regions representing petal junctures, upper surface glabrous, velvety, lower surface sparsely puberulent. Filaments pale virescent, inserted on corolla immediately above apex of ovary, densely lanuginose for several mm. above insertion, then glabrous; anthers 1–2 mm. below corolla mouth, light yellowish green, rotund-elliptic, medifixed. Pollen straw color. Hypogynous disk pale orange. Pistil included, as long as corolla tube; ovary pale greenish, ± conical; style pale greenish; stigma thick discoid, shallowly sulcate. Capsule oval, 8 mm. long, commonly included, on dehiscence valves widely separated, bifid. Seeds numerous, dark brown, about 0.4 mm. long, oval or angular oval, surface shallowly reticulate, its meshes small and ridges sinuous, embryo straight. Chromosome number 12 pairs.

Grown for two seasons in the University of California Botanical Garden along with numerous races of *N. paniculata,* the relationship of *N. Knightiana* to the former species is plain. It is readily distinguishable from *N. paniculata* by the considerably more vigorous habit, ribbed stem, broad, pale dealbate corolla tube and velvety dark green corolla limb. *N. Knightiana* is named in honor of Mrs. Lora J. Knight, of Santa Barbara, California, who has encouraged and generously assisted the work of the University of California Botanical Garden in South America.

EXPLANATION OF PLATES

PLATE 9

Nicotiana Benavidesii, commencing to bloom toward the end of the first winter. (Seed collected Rio Limatambo, cf. p. 137; grown as U.C. B.G. A-058.)

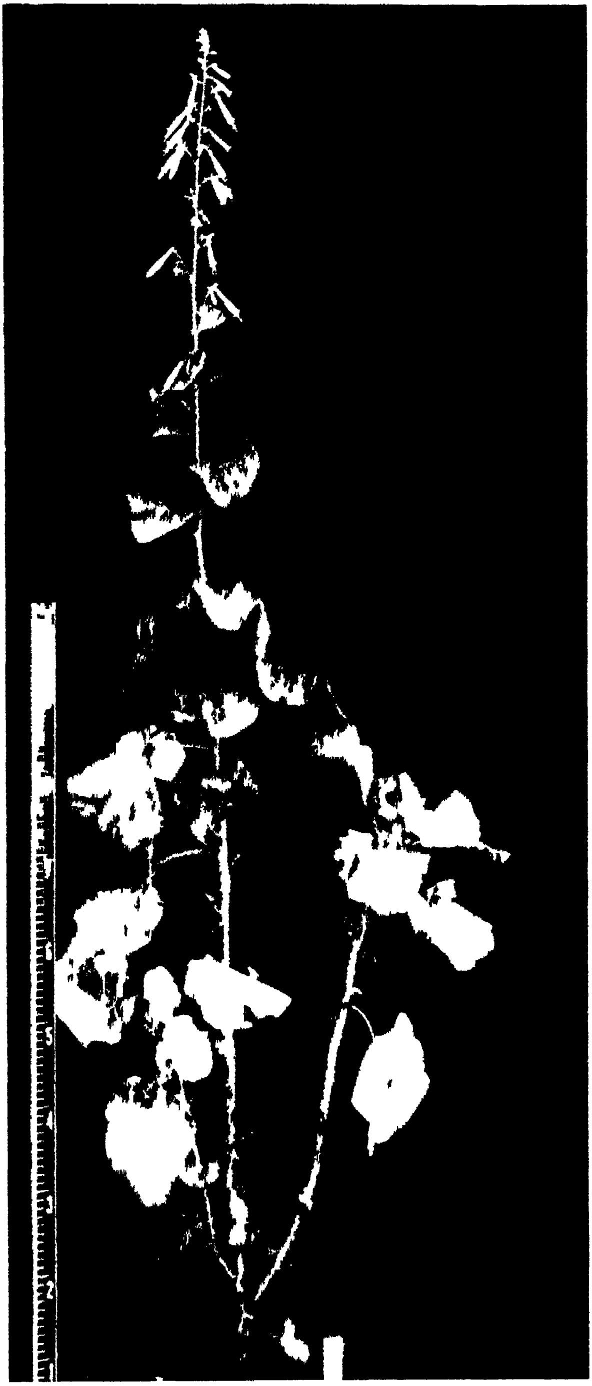


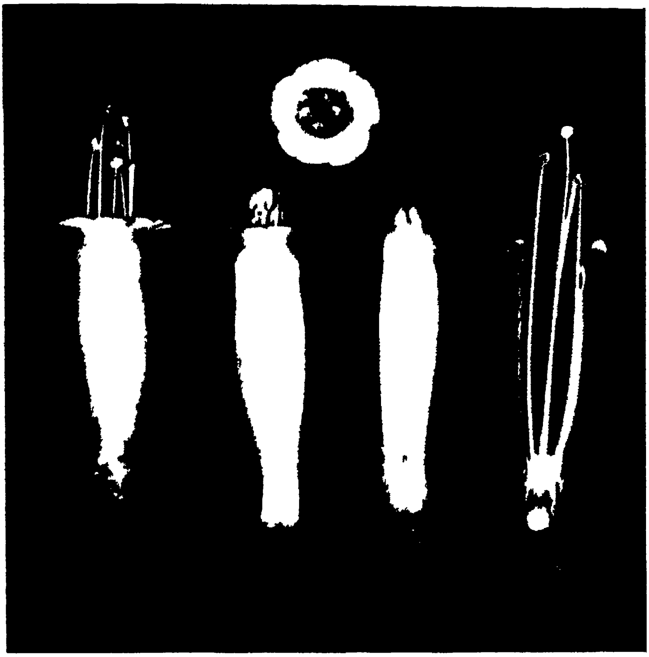
PLATE 10

Nicotiana Benavidesii, detail of a young inflorescence (source as in pl. 9).

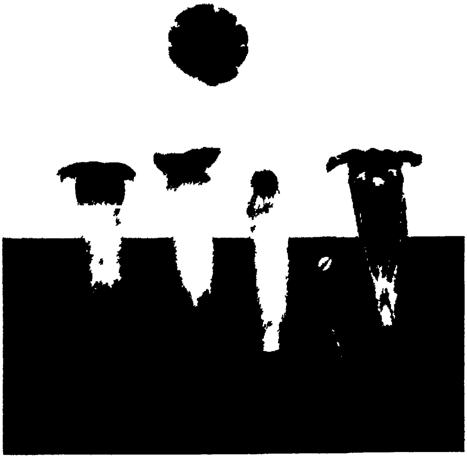
PLATE 12

a. Nicotiana Benavidesii (source as in pl. 9).
b. Nicotiana Knightiana (source as in pl. 11).

× 1. Black paper inserted in the sectioned flower.



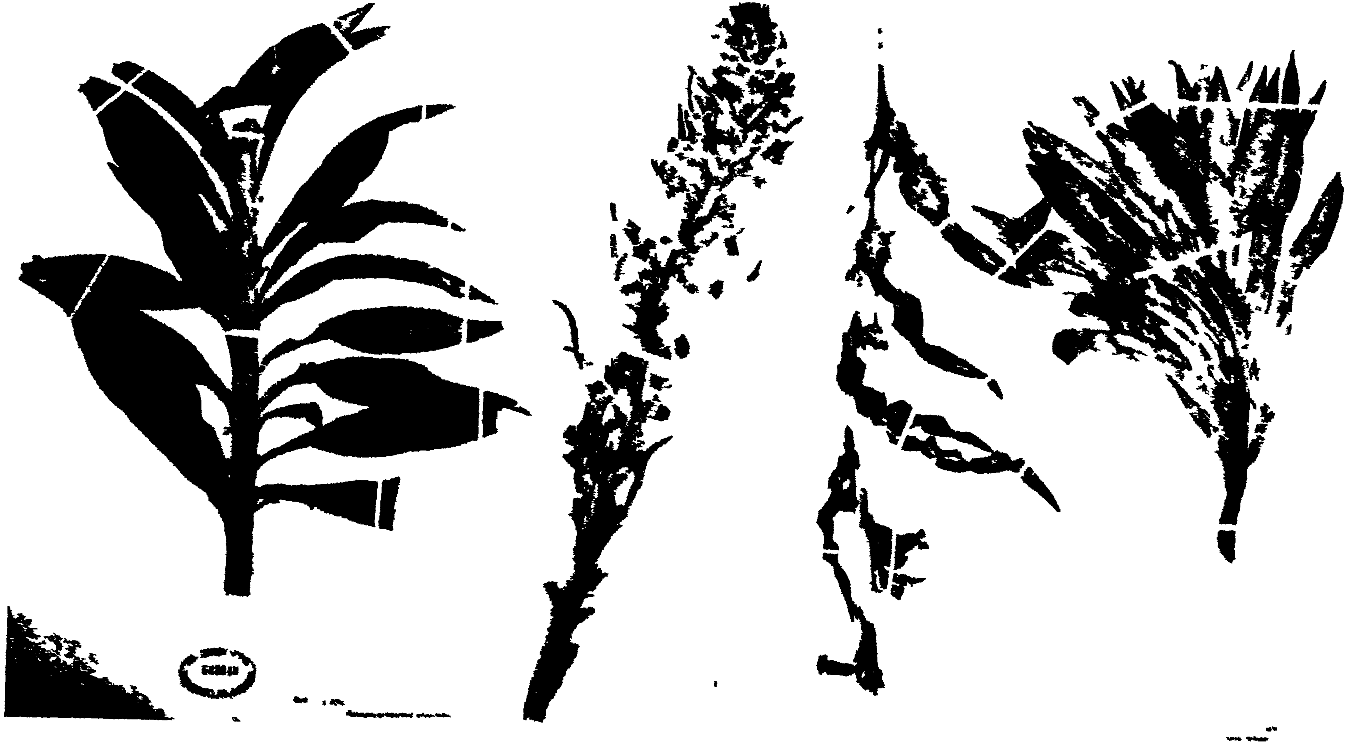
a



b

PLATE 13

Nicotiana thyrsiflora. U.C.H. nos. 583640, 583635, and 583637; cf. p. 138.



CYTOGENETIC EVIDENCES OF NICOTIANA PHYLESIS IN THE ALATA-GROUP

BY

PRISCILLA AVERY

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INTRODUCTION

THE GENUS *Nicotiana* has been shown to consist of a series of species groups distinguished on the basis of morphological characters and cytogenetic relationships (Goodspeed, 1933). The 9- and 10-paired species have been considered to constitute one such phylogenetic unit, the "ALATA-GROUP," in that they possess certain external morphological features in common and are distinct from other species of the genus in respect to chromosome number and morphology. All the other *Nicotiana* species which are native to the Americas have a haploid chromosome number of 12 or 24, and the Australasian species (Wheeler, 1935) of 16, 18, 20, 22, 24, and 32, while *N. alata* Lk. and Otto, *N. bonariensis* Lehm., and *N. Langsdorffii* Weinm. have 9 pairs of chromosomes, and *N. longiflora* Cav. and *N. plumbaginifolia* Viv. have 10. These relatively low chromosome numbers, together with well-marked differences in chromosome morphology, permit critical cytological analysis of the species of the ALATA-GROUP. Furthermore, these species have long been used for genetic investigation (Naudin, 1865; Godron, 1863; Focke, 1881) and evidence is available concerning their crossability, the fertility of their hybrids, and the inheritance of certain of their character differences (East, 1916; Sachs-Skalinska, 1921; Malloch and Malloch, 1924; Brieger, 1930, 1935). Although data concerning the occurrence of the ALATA-GROUP in the wild state in South America are limited, they indicate a distinct and characteristic center of distribution for these species. Thus, we have evidence from (1) distribution, (2) external morphological characters, (3) genetics, and (4) cytology which may be brought to bear upon problems of species origins and relationships within this group. The present report adds to this evidence some new cytological data pertinent to the solution of these problems.

All members of the ALATA-GROUP, with the exception of *N. bonariensis,* have long been in cultivation. They appear to have had a common center of distribution in the southern Brazilian and northern Argentine area, including portions of Uruguay and Paraguay, although they now differ in the reported extent and range of their individual distributions. *N. longiflora* was described by Cavanilles in 1801 from Chile, but at the present time it is abundant in northern Argentina, southern Bolivia, Paraguay, Uruguay, and southeastern Brazil. Furthermore, it has become established in a number of widely separated areas, and appears capable of being introduced in all temperate climates. As it exists in nature and as it is grown in botanical gardens, *N. longiflora* exhibits a rather wide range of variation. Millan (1928) in dealing taxonomically with the Argentinian species of *Nicotiana* recognizes three of the four varieties of *N. longiflora* described by Comes (1899)—varieties *acutiflora, breviflora,* and *pauciflora,* and adds var. *oligantha*. Comes described var. *graciflora* as occurring in Mexico. In the University of California Botanical Garden (U.C.B.G.) many introductions from seed furnished by other botanical gardens and collected from wild plants have been grown. The extremes of variation in all vegetative and floral characters which these cultures have exhibited far exceed the differences between the varieties described by Millan.

The status of *N. plumbaginifolia* as a species is perhaps doubtful since its relationship to *N. longiflora* is obvious. On the other hand, certain *N. longiflora*-like races grown in the U.C.B.G. represent a distinct morphological entity. In their rather delicate, short-lived annual habit, leaf shape, aestivation, small flower, and considerable anthocyanin coloration these races are not approached by the extremes of variation in *N. longiflora,* and correspond to Viviani's description of *N. plumbaginifolia* in 1802. The past and present distribution of this species is somewhat doubtful, but the records indicate that it was introduced into European gardens by the early collectors from some part or parts of the original *N. longiflora* range.

N. bonariensis is definitely known from the wild state, the plants used in the present investigation having been derived from seed which was collected by Herter in the Department of Artigas, Uruguay. Herter (1930) reports collections of this species in ten departments of Uruguay. In distribution, *N. bonariensis* is restricted to northeastern Argentina, Uruguay, and southern Brazil. *N. viscosa* of Lehmann, *N. flexuosa* of Jeffrey, and *N. tristis* of Small are all synonyms of *N. bonariensis,* which was described by Lehmann in 1818. There are well-marked varieties of this species, one of which, var. *spathulata,* was recognized by both Comes and Millan.

Millan (1928) reports that *N. Langsdorffii* occurs in southern Brazil, Paraguay, and the Territory of Misiones, Argentina. Plants from seed collected at Iguassú Falls, Argentina, by the U.C.B.G. Expedition to the Andes (U.C. B.G. 37.18) appear to be the first representatives of this species from the wild to be grown here. The description of *N. Langsdorffii* published by Roemer and Schultes in 1819 ascribes the species to Weinmann *in litt.* and states that Langsdorff collected the seed in Brazil and sent it to Weinmann, but the authorship of *N. Langsdorffii* is in some doubt.

Evidence of the existence of *N. alata* in the wild state at the present time has not been obtained, although Millan says that it occurs in southern Brazil, Paraguay, Uruguay, and in Argentina from Misiones to Concepcion del Uruguay, and Herter (1930) reports collections in five departments of Central Uruguay. Link and Otto in their description of *N. alata* published in 1828 say that the Hortus Regius Botanicus Berolinensis obtained the seed of this plant from Sello in Brazil in 1827. Comes (1899) recognized *N. affinis* T. Moore as equivalent to *N. alata* var. *grandiflora,* and considered *N. persica* Lindl. to be a variety of *N. alata* cultivated in Persia. *N. brasiliensis* Lk. and Otto and *N. decurrens* Agardh are also synonyms of *N. alata,* according to Comes.

There are two other species which should be considered as members of this group, *N. Forgetiana* Hort. Sand. ex Hemsley and *N. Sanderae* Hort. ex Watson. *N. Forgetiana* was described in the Gardener's Chronicle (1903, p. 256) as a Brazilian species bearing numerous red flowers. Sander and Sons crossed it with *N. affinis* (*N. alata* var. *grandiflora*) and obtained the hybrids known as *N. Sanderae* which they introduced into trade. Hemsley (1905) described and figured *N. Forgetiana* from specimens furnished by Sander and Sons, and pointed out the similarity of this species to *N. bonariensis* Lehm. There is no evidence that *N. Forgetiana* has been collected a second time, and probably the red-flowered races so named, as well as many white-flowered ones, have come from the original cross. Herbarium and genetic evidence indicate that the red color factors and other characters determined to be present in *N. Sanderae* (Sachs-Skalinska, 1921) were introduced into *N. alata* stock by the closely related red-flowered species *N. Forgetiana*. Because of this known derivation of *N. Sanderae* from *N. alata* and the present unavailability of *N. Forgetiana, N. alata* has been used to represent both *N. Sanderae* and *N. Forgetiana*. Comes (1899) considers *N. commutata* Fisch. and Meyer as the variety *grandiflora* of *N. Langsdorffii*, and *N. pseudo-decurrens* Steud. and *N. decurrens* Tausch. as synonyms of the variety *longiflora* of the same species. Both of these varieties are unquestionably segregates from the cross *N. Langsdorffii* × *N. alata*, and not equivalent to *N. Langsdorffii* Weinm.

With respect to morphological characters, the five valid species, *N. alata, N. bonariensis, N. Langsdorffii, N. longiflora,* and *N. plumbaginifolia,* have in common a somewhat low, herbaceous habit in contrast to the semiarborescent or at least sizable character of many species of *Nicotiana* such as *N. tomentosa, N. glauca,* and *N. glutinosa*. Indeed, apart from the *corymbosa* aggregation (Goodspeed, 1933), the genetic group under discussion is more strictly herbaceous than any other South American one. In general, the five species may be called annuals, but they vary from short-lived annuals to limited perennials. Thus in cultivation *N. bonariensis* may not flower until the second year, and the remnants of the massive and enduring rosettes of *N. longiflora* varieties may, under continued favorable environmental conditions, reproduce the individual for another year or more. Plants of *N. alata* are less apt to survive a second year than are those of the longer lived *N. longiflora* varieties, but all three species, *N. bonariensis, N. longiflora,* and *N. alata,* can be held successfully in greenhouse pot culture for a number of years. In field culture *N. plumbaginifolia* is very short lived and dies some weeks after flowering. Of rapid early growth and early anthesis, *N. Langsdorffii* is not in as vigorous condition toward the end of the first season as are *N. bonariensis* and *N. longiflora,* but may live a second year under favorable greenhouse conditions.

All five species establish a rosette which is persistent only in *N. longiflora*. Characteristic for the group is the lateral branching from the base of the mature plant to produce a somewhat bushy habit in all species except *N. plumbaginifolia*. Leaf shape is somewhat variable, but in all of them the leaf is sessile and more or less auriculate.

In all species except *N. Langsdorffii* a zygomorphic flower form occurs, the corolla lobes being deeply incised, with three lobes above and two below. This zygomorphism is most strongly expressed by *N. bonariensis* and *N. alata* and less so by *N. longiflora* and *N. plumbaginifolia.* The corolla limb of *N. Langsdorffii* is entire, with the lobes slightly notched at the apex, the sinuses scarcely evident, and a gibbous ring pronounced on the upper surface of the tube. The green color of *N. Langsdorffii* with entire absence of anthocyanin is in contrast to the other four species, whose flower color is a chalky, creamy, or greenish white with varying amounts of purple on the under surface of the limb and on the corolla tube. Flower size characters show the widest range of variation in *N. longiflora* and *N. alata* and are quite constant in *N. bonariensis, N. Langsdorffii,* and *N. plumbaginifolia.* The blue pollen color of *N. Langsdorffii* is unique in the genus *Nicotiana.*

If similarities in external morphology be taken as an index to the degree of relationship between any two species, we have within this group of five species an expression of different degrees of affinity, the group as a whole being morphologically delimited from other species groups in the genus. However, a clear picture of their evolution and relationship cannot be obtained by a study of external morphology alone, for, as has been pointed out, the union of these five species into a single genetic group is based as much upon cytogenetic as it is upon morphological evidence. The ALATA-GROUP is, then, a small, distinct assemblage of species whose relationship to one another can best be evaluated by supplementing the evidence of similarities and differences in external morphology with a comparative study of chromosome number, size and shape, and the determination of the amount and kind of conjugation occurring between the chromosomes of the species in their F_1 hybrids.

The significance of such cytological evidence for the problem under discussion deserves consideration. Where polyploidy or hybridization are not involved, the major processes known to be operative in species differentiation are chromosome reorganization and gene mutation. While it may be that the former process underlies the latter (Muller, Prokofyeva, and Raffel, 1935), nevertheless, so far as the origin of distinctions in visible chromosome structure is concerned the two may be taken to proceed independently and concurrently (cf. Cleland, 1935, p. 341). A comparison of the genoms of two related species will reveal the extent of gross alterations in chromosome organization during their differentiation from each other, and a comparison of their external morphologies will indicate roughly the extent of accumulation of gene mutations in their evolution from a common ancestral stock. However, the conclusions reached from these two comparisons alone may need modification, for structural alterations may occur in chromosome complements without being visible and gene mutations which affect certain conspicuous or important morphological characters may be evaluated as evidence of greater differentiation than they represent. Moreover, if structural chromosome alterations give rise to gene mutations, the adding together of the products of the two processes may not be justified. Therefore it is important to supplement the conclusions reached on these two bases with a study of meiotic chromosome behavior in hybrids. Usually, such evidence gives definite indication of the extent to which species have accumulated differences in genes and genic organization. Although nonhomologous chromosomes may conjugate in abnormal individuals or under abnormal conditions (McClintock, 1933), regular pairing of chromosomes can take place only if the two sets of chromosomes concerned contain similar genes, similarly organized (cf. Cleland, 1935, p. 343). Thus, if conjugation occurs between chromosomes of different genoms, its extent and kind may be an index of degree of similarity in genic constitution and organization and assist in evaluating the evolutionary rôles played by gene mutation and alterations in genic organization.

Acknowledgments

For materials and facilities used, for advice and interest throughout this investigation, and for assistance in the preparation of the manuscript, I am indebted to Professor T. H. Goodspeed. I would acknowledge also the value of studies of the complement of *N. Langsdorffii* made by Lillian J. Raup.

MATERIAL AND METHODS

The stocks used in making the interspecific hybrids referred to here represent lines maintained at the U.C.B.G. by self or sister pollinations, most of them having been grown for many generations. Two different lines of *N. longiflora* and *N. alata* were used, so that seven sources are represented by the five species under investigation (cf. table 1). The *N. Langsdorffii* stock had been grown for twenty-nine years in pure line, the original source being the Jardin Botanique, Geneva. The *N. plumbaginifolia* stock, which had been grown in pure line for twenty-five years, was originally obtained from O. Comes at Portici. One of the *N. alata* var. *grandiflora* stocks had been maintained by sister pollinations for ten years from seed obtained from a local garden plant, and the second stock of *N. alata,* used in the cross with *N. bonariensis,* was obtained from the R. Istituto Sperimentale Coltivazioni Tabacchi at Scafati, and had been grown only one year. Except in the cross of *N. longiflora* with *N. plumbaginifolia,* a stock of *N. longiflora* var. *breviflora* was used, which was obtained through the Museo Nacional, Rio de Janeiro, from a collection by C. V. Greire, and had been grown at the U.C.B.G. for three years. In the cross with *N. plumbaginifolia,* a typical *N. longiflora* obtained from the Institute of Applied Botany and New Cultures of the U.S.S.R. was used. It, also, had been grown for three years, and proved uniform in morphological characters from the first. *N. bonariensis* was grown from seed collected by Herter (no. 82755) in the Department of Artigas, Uruguay. The original population showed much segregation, and succeeding populations although less variable have not yet reached complete homozygosity. This is because the natural self-sterility of the species, apparently similar to that in *N. alata,* requires its maintenance by sister pollinations.

Somatic chromosomes were studied in root tips fixed in the chromacetic formalin solution of Hollingshead and Babcock (1930, no. 1, p. 3) and stained with iron haematoxylin. PMC and microspore mitoses were studied in iron aceto-carmine smears, although permanent smears using chromacetic formalin followed by iodine gentian-violet were used to verify observations made on the temporary smears. Whenever possible, the drawings were made of PMC in which the orientation of chromosomes at diakinesis and IM did not interfere with their interpretation. However, in several of them (figs. 4, *a, c, f*; 7, *a, b*; 8, *i*; 9, *a, b, c*; 10, *f*; 11, *e*) it has seemed advisable to draw one or a few originally superimposed units in one plane.

TABLE 1

SOURCE OF STOCKS USED IN ALATA-GROUP HYBRIDS

Species	Variety	Accession no., U.C.B.G.	Source
1. *N. alata*	*grandiflora*	22–3	Garden plant, Berkeley, 1922
2. *N. alata*	*grandiflora*	31–13	R. Ist. Sper. Coltiv. Tab., Scafati, 1931
3. *N. bonariensis*	....	28–51	Coll. G. Herter no. 82755, Artigas, Uruguay, 1928
4. *N. Langsdorffii*	....	02–22	Jard. Bot., Geneva, 1902
5. *N. longiflora*[a]	*breviflora*	29–20	Coll. C. V. Greire (Mus. Nac., Rio de Janeiro) 1929
6. *N. longiflora*[b]	....	29–45	Inst. Appl. Bot. and New Cult., Leningrad, 388/90598, 1929
7. *N. plumbaginifolia*[c]	....	07–9	O. Comes, R. Sc. Sup. d'Agric., Portici, 1907

[a] Received as *N. acutiflora* var. *breviflora*.
[b] Received as *N. noctiflora*.
[c] Received as *N. noctiflora* var. *albiflora*.

CHROMOSOME NUMBER AND MORPHOLOGY IN FIVE SPECIES

The nature of the karyotype serves to divide the five species of the ALATA-GROUP into two sections, *N. longiflora* and *N. plumbaginifolia* forming a 10-paired group, and *N. alata, N. Langsdorffii,* and *N. bonariensis,* a 9-paired group. With respect to the morphologies of the chromosomes, there is a striking difference in the karyotypes of these two groups, the 10-paired species having only one morphological type of chromosome, and the 9-paired species at least four distinct types (cf. fig. 1).

Chromosome morphology in *N. longiflora* was studied by Hollingshead (1929), and her conclusions have been confirmed in the present investigation. All the 20 somatic chromosomes have subterminal insertion regions, making them "headed" chromosomes (Lewitsky, 1931*a*). There is a continuous slight variation in length from the longest to the shortest, with an average of 3.3 μ. The uniformity in position of the insertion region gives a characteristic con-

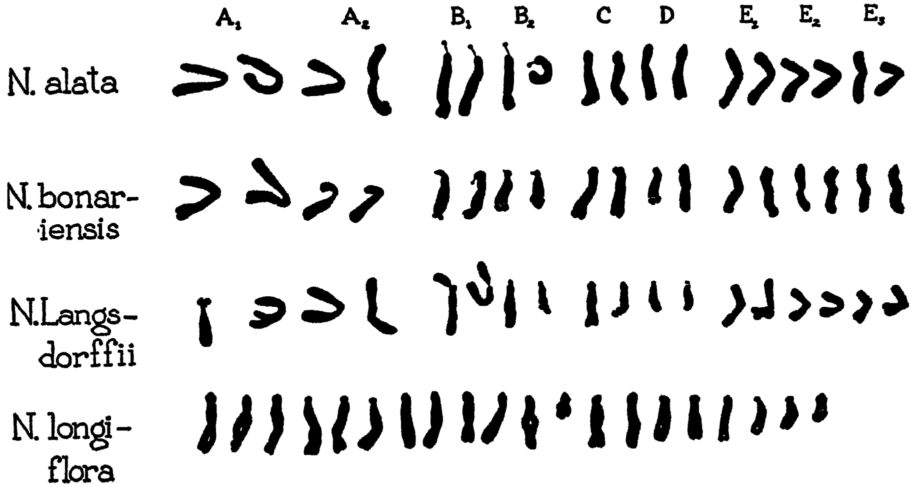

Fig. 1. Somatic chromosomes of the 9- and 10-paired species of *Nicotiana*, showing the basic karyotype with specific distinctions in the 9-paired species, and the contrasting karyotype of the 10-paired species *N. longiflora.* × 1915. A, long chromosomes, median insertion region (A_2 of *N. bonariensis*, submedian). B, long chromosomes, subterminal insertion region, and small, proximal satellite (B_1 of *N. Langsdorffii*, large satellite). C, chromosomes of approximately the same length as the B chromosomes less the satellites, subterminal insertion region. D, chromosomes shorter than C, subterminal insertion region (D of *N. alata* more submedian; D of *N. Langsdorffii* very small with small satellite). E, shorter chromosomes, slight variation in length, median or submedian insertion region.

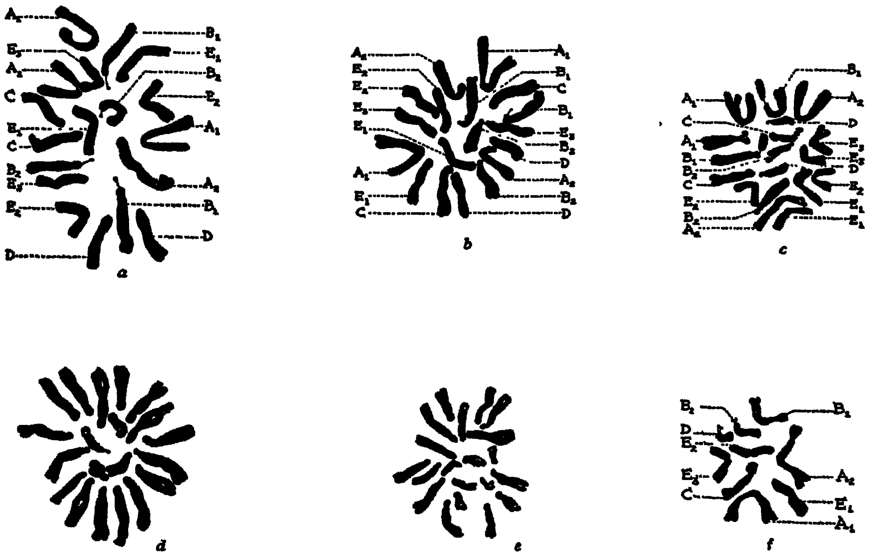

Fig. 2 *a–e*, somatic metaphase plates from root tips of: *a*, *N. alata; b, N. bonariensis; c, N. Langsdorffii; d, N. longiflora; e, N. plumbaginifolia. f,* first microspore mitosis in *N. Langsdorffii.* Letters indicate chromosomes of the morphological types explained in figure 1. × 1915.

figuration to the somatic metaphase plates, 15 to 16 chromosomes lying like the spokes of a wheel around the center of the plate where 4 or 5 chromosomes, usually the shorter ones, lie in a plane at right angles to the others, forming a "hub" (fig. 2, *d*). This configuration, chromosome number, and uniformity of subterminal insertion region mark the *N. longiflora* genom as distinct from that of all other species in the genus except *N. plumbaginifolia.*

Hollingshead (1929) and Sarana (1934) reported finding no chromosomes with proximal satellites, but, rather, short chromosomes with distinct distal constrictions forming satellite-like knobs, and with this the observations of the present investigator agreed. Whether the distal constrictions are associated with nucleolus-producing regions is not certain from the evidence at hand, but such association is suggested by diakinesis figures in which a small bivalent is attached to the nucleolus near an almost terminalized chiasma (fig. 5, *a*). At least four chromosomes in the somatic complement produce nucleoli, for four nucleoli with small attached pycnotic regions are often visible in mitosis at late telophase and early resting stage (fig. 3, *a*). In later resting stages and early prophases fusion may give rise to one or two nucleoli. In the prophases of meiosis also, two pairs of chromosomes may be associated with the nucleolus, one a smaller and the other a medium-sized pair. Two pairs of nucleolus-producing chromosomes have also been found to occur in *N. longiflora* by Resende (1927). He describes one pair as having proximal and the other as having distal satellites. Although the proximal satellites have been inadequately demonstrated in the present material (fig. 2, *d*), Resende's interpretation is undoubtedly correct.

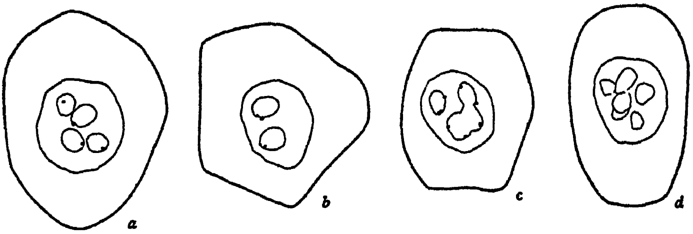

Fig. 3. Nucleoli in the resting stage of mitoses in root tips of: *a, N. longiflora,* four nucleoli, each with associated pycnotic region; *b, N. plumbaginifolia,* two nucleoli at a stage corresponding to that of the nucleus in *a; c, N. alata,* four nucleoli, three of which have fused to form a single large nucleolus; *d, N. Langsdorffii,* six nucleoli, of three different sizes. × 1133.

Hollingshead (1929) states that "the fiber attachment of certain of the long chromosomes may be terminal," since she was unable to obtain adequate evidence of the presence in these chromosomes of subterminal insertion regions. Though all the chromosomes in a single metaphase plate rarely show well-marked subterminal constrictions, yet the majority always do, and it is certain that although some insertion regions are very close to the proximal end there are no strictly terminal ones.

N. plumbaginifolia, which resembles *N. longiflora* in external morphology, has the same number of somatic chromosomes (20) and the same uniformity of subterminal insertion region, with the same characteristic wheel-like arrangement of the chromosomes at metaphase (fig. 2, *e*), but the chromosomes of *N. plumbaginifolia* were found to be smaller, both shorter and narrower, than those of *N. longiflora.* Further comparative studies are required before it is certain that such a cytological basis for distinction between the two species exists. A further cytological distinction is the presence of only two nucleolus-producing chromosomes in somatic mitoses of *N. plumbaginifolia* and the appearance of only one or two nucleoli (fig. 3, *b*) at the stages of mitosis in which two to four are usually present in *N. longiflora.*

The smaller plant body and shorter life duration of *N. plumbaginifolia* as contrasted with *N. longiflora* may be directly correlated with smaller chromosome size and fewer nucleoli. In this connection, Babcock (1936) has noted with respect to related four-paired *Crepis* species that the differentiation of smaller-sized species has been accompanied by the differentiation of complements of smaller chromosomes. Further, Delaunay (1926) has noted that species with smaller chromosomes are reduced in size as compared with related species with larger chromosomes, owing to a correlation of length of meristematic regions with chromosome size. Such correlations would account for the difference between *N. longiflora* and *N. plumbaginifolia* in chromosome size and size of plant body.

By contrast with the single type of chromosome morphology exhibited by the karyotype of the two 10-paired species, the three 9-paired species possess a karyotype with at least four types of chromosomes (fig. 1). Although distinctions in chromosome morphology differentiate these three species, it is noteworthy that the same fundamental karyotype is clearly evident in each. All three have two pairs of large chromosomes with median insertion regions, designated A_1 and A_2; two pairs with subterminal insertion regions and proximal satellites, designated B_1 and B_2; two pairs with subterminal insertion regions differentiated chiefly on the basis of length into C and D chromosomes; and finally, three pairs of shorter chromosomes with median or submedian insertion regions, designated E_1, E_2, and E_3.

Conspicuous because of length (6.5 μ) and characteristic V-shape in the genoms of all the 9-paired species are the A chromosomes. In *N. alata* it has not been possible to establish any morphological distinctions between the A_1 and the A_2 pairs (Avery, 1929). Sometimes tertiary constrictions (Lewitsky, 1931*b*) are prominent about three-fourths of the distance from the insertion region to the ends of the arms (cf. Sarana, 1934), and it is probable but not certain that all eight arms of the *N. alata* A_1 and A_2 chromosomes have constrictions at this point. Trisomic types containing A chromosomes in triplicate have been obtained in *N. alata,* and the fact that two such types have differed phenotypically indicates that the two pairs of these chromosomes are of different genic constitution (Avery, 1930). In *N. Langsdorffii* one of the two pairs is slightly shorter than the other and shows a more submedian insertion region—a morphological distinction that usually suffices to differentiate these pairs in somatic plates. In *N. bonariensis,* in contrast to *N. alata* and *N. Langsdorffii,* there is only one large V-shaped (A_1) pair, the other pair being replaced by chromosomes which have one arm corresponding in length to the *N. alata* A chromosomes, the other arm being reduced to one-fourth the length in *N. alata*, producing a J-shaped chromosome. This A_2 pair in *N. bonariensis* is not duplicated in the *N. alata* or *N. Langsdorffii* complements and is a specific point of cytological distinction in this species.

In these three 9-paired species there are three additional pairs of V-shaped chromosomes designated E, with median or slightly submedian insertion regions, all much smaller than the A chromosomes just described. Sufficient difference may exist to distinguish morphologically between these E pairs in some, if not in all, the species, but they have been treated as a group because their identification with this group is much more certain than any distinctions between its members. It may be noted, however, that one pair is slightly longer than the other two, and has a somewhat submedian rather than a strictly median insertion region in all three species, so that in *N. alata,* where these E chromosomes all approximate 4 μ in length, with each arm 2 μ, this E_1 pair has one arm somewhat longer than 2 μ.

The two B pairs of chromosomes with subterminal insertion regions bear proximal satellites in all three species. In *N. alata* they are indistinguishable, both pairs being long rodlike chromosomes, 4.5 μ in length without the satellite, and 5.5 μ when the small satellite separated by a distinct thread is included. The satellite in *N. alata* is so small that it may readily be obscured, and only rarely are all four satellites evident. In *N. bonariensis* there are four satellited chromosomes very similar to those in *N. alata.* In *N. Langsdorffii* two (B_1) resemble the *N. alata* pairs in being long rods with subterminal insertion regions, but their satellites, instead of being small, are almost as large as small chromosomes. The satellite is separated from the body of the chromosome by a distinct thread, so that when this chromosome is bent at the insertion region and is stretched out its full length it is almost as long and V-shaped as the A chromosomes. This pair suggests the satellited pair figured for *Crepis setosa* by Hollingshead and Babcock (1930), and specifically identifies the genom of *N. Langsdorffii.* Another satellited pair in *N. Langsdorffii* does not resemble this B_1 pair or those in *N. alata* or *N. bonariensis,* for it is the shortest chromosome pair in any of the 9-paired species. In satellite size, however, it does resemble the B chromosomes of the two species. This chromosome is roughly two-thirds the length of the main shaft of the B_1 pair. It has been designated D rather than B because it is the only chromosome in *N. Langsdorffii* whose morphology does not place it in some other group. A third pair of chromosomes with satellites in *N. Langsdorffii* must have partly lost its nucleolus-producing function (cf. McClintock, 1934), since this pair shows a satellite-like body which is close to the head of the chromosome but seldom separated from it by a distinct thread. In all other respects it is morphologically closer to the B chromosomes in *N. alata* and *N. bonariensis* than are the two more distinctly satellited chromosomes in *N. Langsdorffii* (B_1 and D), and has therefore been designated B_2. Although the nucleolus-producing function of these chromosomes has not been investigated in detail, it is significant that whereas four nucleoli is the maximum number observed to occur in the somatic nuclei of *N. alata* (fig. 3, *c*), five or six have been found in corresponding nuclei of *N. Langsdorffii* (fig. 3, *d*).

The remaining two pairs in the 9-paired species possess subterminal insertion regions, without satellites. In *N. alata* one of these pairs (C) is the same length as the B chromosomes less the length of the satellite and its thread (4.5 μ) with the insertion region likewise subterminally placed, and the other (D) is shorter (3.5 μ) with an almost submedian insertion region. In *N. bonariensis* there are two pairs which correspond closely to the two in *N. alata* except that the D chromosome has a more subterminal insertion region. *N. Langsdorffii* has one pair similar to the C chromosome in *N. alata*. The remaining small satellited pair in *N. Langsdorffii*, already mentioned, is thus the probable homologue of the D chromosomes in *N. alata* and *N. bonariensis*.

In figure 1 the chromosomes present in the metaphase plates of the 9-paired species (fig. 2) have been grouped according to their morphological types. The basic karyotype is evident, together with individual deviations from the pattern. Thus, the genom of *N. bonariensis* shows only one striking morphological difference from that of *N. alata*, its large J-shaped A_2 pair corresponding to the large V-shaped A_2 pair of *N. alata*, whereas *N. Langsdorffii* shows two conspicuous differences from *N. alata* in its B_1 and D chromosomes, and a less prominent difference in its A_1 pair. Relatively few reorganizations could account for these visible differences between the genoms of the 9-paired species, and these specific differences, as well as the basic similarity, are important evidences of the methods of speciation operative in the ALATA-GROUP.

CHROMOSOME BEHAVIOR IN THE SPECIES

Some features of bivalent configuration at diakinesis and IM[1] have been studied in *N. alata, N. bonariensis, N. Langsdorffii*, and *N. longiflora*. In all these species the nonconjunction of one pair of chromosomes has been found to occur occasionally (Ruttle, 1937; Hollingshead, 1929), and is probably related to a low chiasma frequency in certain bivalents rather than to structural differences between homologous chromosomes. However, as both *N. alata* and *N. bonariensis* are self-sterile species, usually maintained only through sister pollinations, it is possible that "structural hybrids" occur even though there are no visible morphological differences between homologous chromosomes.

In *N. alata*, bivalents composed of the four morphological types of chromosome above described can be identified by differences in length and in position of insertion regions (fig. 4, *a–c*). The long A chromosomes with their median insertion region usually form two chiasmata, one in each arm, and the bivalent configuration at late diakinesis and first metaphase depends upon the extent of terminalization of these two chiasmata. Usually, both are completely terminalized to give a ring bivalent, the typical configuration at IM. At times, however, only one chiasma is completely terminalized. Rarely, more than two chiasmata occur, and sometimes a chiasma is formed in one arm only, giving the bivalent a "V" or "U" shape if this single chiasma is completely terminalized, or an "X" or " + " shape if unterminalized.

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[1] IM, IA, IT = metaphase, anaphase, and telophase, respectively, of the first meiotic division; IIM, IIA, IIT = corresponding stages of the second meiotic division.

The other seven pairs cannot be distinguished in meiosis on the basis of chromosome size, which prevents their being identified at diakinesis and IM

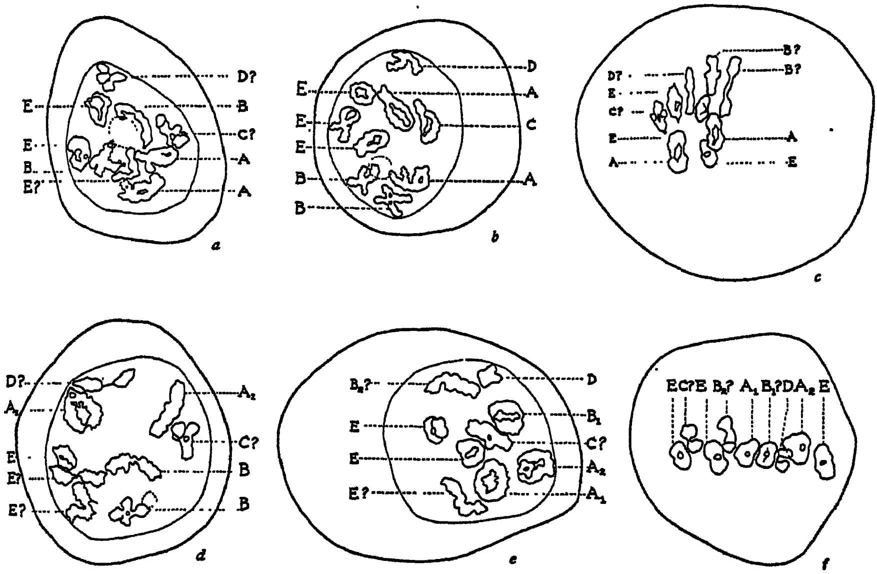


Fig. 4. Bivalent configurations and chiasma frequency in the 9-paired species. Chromosomes which can be identified by size or behavior are labelled as in figures 1 and 2. Where identification is uncertain a question mark has been used. *a–c*, *N. alata:* *a*, diakinesis, 13 chiasmata, of which 6 are terminal = 13/6 Xta; *b*, diakinesis, 14/6 Xta; *c*, early IM, 14/12 Xta. *d*, *N. bonariensis*, diakinesis, 11/8 Xta. *e*, *f*, *N. Langsdorffii*, *e*, diakinesis, 14/9 Xta; *f*, IM, 15/13 Xta. × 1300.

as readily as the A chromosomes. Nevertheless, from late diplotene to IM, these seven pairs can be separated into three groups on the basis of bivalent configuration. Thus, three bivalents usually have two chiasmata which terminalize by late diakinesis to give small ring bivalents. The correspondence in position and behavior of these chiasmata to those occurring in the large A bivalents indicates that they represent the usual configuration assumed by the three E pairs of smaller chromosomes with median insertion regions. The other four pairs usually form a single chiasma, which, by late diakinesis, is most frequently interstitial in two pairs and terminalized in the other two. In diplotene and early diakinesis two of these four pairs are associated with the nucleolus, and usually at least one pair retains this association until mid- or late diakinesis. These two bivalents must be composed of the satellited B chromosomes (cf. Heitz, 1931; McClintock, 1934), each of which possesses a nucleolus-producing region. A study of these bivalents during diakinesis showed that the single chiasma formed might be either interstitial or terminal, but was more frequently interstitial at the earlier stages where their association with the nucleolus was clearest (26 interstitial; 18 terminal). In many PMC, the single chiasma in one of the two pairs at mid-diakinesis was terminalized and in the other it was interstitial (fig. 4, *a*). It is probable that at the later stages these bivalents may have a single terminal chiasma more frequently than an interstitial one, but the absence of the nucleolus in late diakinesis makes their certain identification impossible. The remaining two bivalents, each with a single chiasma, are composed of C and D chromosomes with subterminal insertion regions but with no nucleolus-producing regions or satellites. Sometimes the somewhat smaller size of the D as compared with the C chromosomes is apparent, but it cannot be relied upon to distinguish these chromosomes. Each of the two pairs may have its single chiasma in either an interstitial or a terminal position at diakinesis. The difference in configuration at late diakinesis where two of these four pairs show terminal and two interstitial chiasmata would seem to depend not on association with the nucleolus (Darlington, 1936), but rather on chance, the point of chiasma formation determining whether it becomes terminalized by late diakinesis. The pairs in which the single chiasma is interstitial at diakinesis are of particular interest because of the distinctness with which the chiasma can be seen and its terminalization followed to metaphase. Thus at mid-diakinesis the bivalents are ×-shaped, the exchange of chromatids often being visible, while at late diakinesis terminalization has made them + -shaped, and at metaphase they are usually rods, often with a median "bump" to indicate that the chiasma is not yet completely terminalized.

Although the configurations described above—two large ring bivalents, three small ring bivalents, two bivalents with a single terminal chiasma, and two with a single interstitial chiasma (fig. 4, *c*)—can be considered typical of *N. alata* at late diakinesis and IM, there are many deviations from this typical pattern. The small chromosomes with median insertion region often fail to form a chiasma in one arm, so that by late diakinesis they have only a single terminal chiasma and are therefore indistinguishable from the B, C, and D pairs, especially after the B pairs no longer show association with the nucleolus. Any of the four pairs with a subterminal insertion region (B, C, and D) may occasionally form two chiasmata. When one of them is in the short arm, the resulting ring bivalent may not be distinguishable from the E pairs with median insertion region. We can, then, account for the occurrence of an average of 13.4 chiasmata at diakinesis in *N. alata* (cf. table 2) by the formation of two chiasmata in each of the A pairs to give 4 chiasmata; two in each of the three E pairs, with an occasional failure of chiasma formation in one arm to reduce the total chiasmata for these pairs from 6 to 5 +; and a single chiasma in each of the two B, the C, and the D pairs, with occasional formation of two chiasmata in some of these pairs to increase their chiasmata to 4+. We thus have 4, 5 +, 4+ to give an average of 13.4 chiasmata per PMC.

N. bonariensis has a lower chiasma frequency (11.2) than *N. alata* (cf. table 2). Although the data are not numerous this decrease in chiasma frequency is significant in that it can be related to distinctions in chromosome mor-

TABLE 2

CHIASMA FREQUENCY AT DIAKINESIS AND IM IN 9- AND 10-PAIRED SPECIES OF NICOTIANA

Species	Chiasma frequencies																			Total PMC	Ave. chiasmata per PMC	Ave. chiasmata per bivalent
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	19				
1. *N. alata;* n=9																						
Total	...	...	...	...	...	...	...	...	...	...	1	3	5	4	4	...	...	...	...	17	13.4	1.5
Terminal	...	...	...	...	...	2	2	3	3	3	2	2	...	...	...	...	...	...	...	17	9.0	1.0
2. *N. bonariensis;* n=9																						
Total	...	...	...	...	...	...	...	...	2	3	9	4	1	2	...	...	...	...	...	21	11.2	1.2
Terminal	...	...	...	1	6	3	5	4	2	...	...	...	...	...	...	...	...	...	...	21	6.5	0.7
3. *N. Langsdorffii;* n=9																						
Total	...	...	...	...	...	...	...	...	...	...	...	...	2	9	4	...	...	...	...	15	14.1	1.6
Terminal	...	...	...	...	...	...	...	...	1	1	2	5	4	2	...	...	...	...	...	15	12.1	1.3
4. *N. longiflora;* n=10																						
Total	...	...	...	...	...	...	...	...	...	1	2	2	2	1	2	1	2	1	...	14	13.9	1.4
Terminal	1	3	1	1	2	2	1	3	...	...	...	...	...	...	...	...	...	...	...	14	4.8	0.5

phology between the two species. The large J-shaped A_2 pair in *N. bonariensis* usually forms only a single chiasma instead of the two characteristic of the A_2 pair in *N. alata* (fig. 4, *d*). Where two large rings are present at IM, one (A_1) is distinctly larger than the other. In contrast with *N. alata,* ring bivalents were also found to be less frequent among the E chromosomes of *N. bonariensis,* the latter usually forming only one small ring whereas two or three are present in the former. In *N. bonariensis,* as in *N. alata,* the four pairs with subterminal insertion regions (B_1, B_2, C, D) tend to form only a single chiasma, which is frequently not terminalized by metaphase. The types of bivalent configurations found in these two 9-paired species are thus similar but differ in frequency of occurrence.

The study of a few PMC at IM in *N. Langsdorffii* showed that here, also, the same configurations occur but that in contrast to *N. bonariensis,* where the chiasma frequency was reduced below that of *N. alata,* it is here increased, the average being 14.1 chiasmata per PMC (table 2). Two chiasmata were always formed in each of the A pairs, and another pair equaling in size the smaller A pair usually formed two chiasmata (fig. 4, *e, f*). This must be the B_1 pair, with large satellites of sufficient length to permit the formation of a chiasma within them. This difference in behavior of the B_1 chromosomes accounts for the increased chiasma frequency in *N. Langsdorffii* as compared with that of *N. alata.*

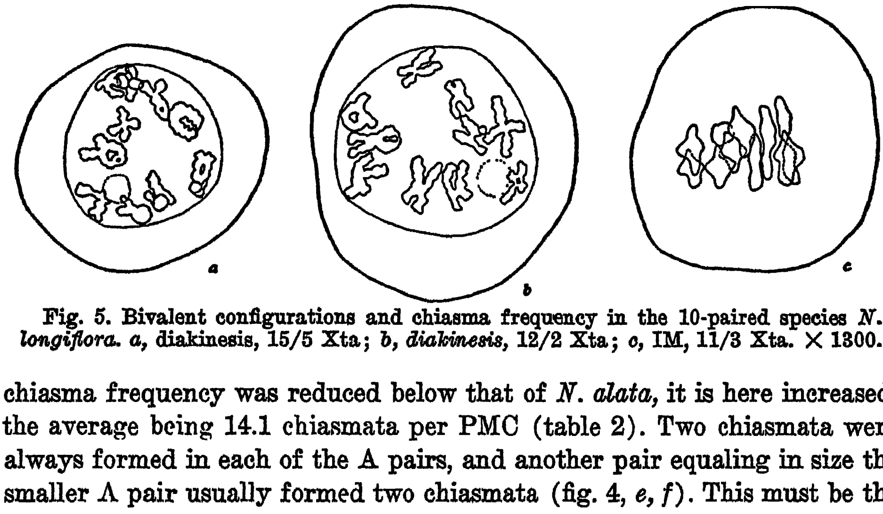


Fig. 5. Bivalent configurations and chiasma frequency in the 10-paired species *N. longiflora. a,* diakinesis, 15/5 Xta; *b, diakinesis,* 12/2 Xta; *c,* IM, 11/3 Xta. × 1300.

Three different lines of *N. longiflora* have been studied at diakinesis and IM, and the evidence in hand indicates that there is a difference in chiasma frequency between one of these strains and the other two. Thus, for one line the average chiasma frequency per PMC is 15.7, and for the two others it is 12.1, the average for all three being 13.9 (table 2).

In *N. longiflora* only one ring bivalent with two terminal chiasmata usually occurs at diakinesis and IM (fig. 5, *a*), although two or more bivalents may have both an interstitial and a terminal chiasma (fig. 5, *b*). The fact that the majority of the bivalents in this species have a single interstitial or terminal chiasma is in agreement with the type of configuration to be expected wherever chromosomes with subterminal insertion regions occur, provided chiasma formation and behavior are similar to that of corresponding pairs in *N. alata.*

The occurrence of a few ring bivalents in *N. longiflora* is important as indicating that the configuration characteristic of chromosomes with a median or submedian insertion region may also be formed by those whose insertion region is subterminal. The fact that six to eight of the ten pairs of chromosomes in *N. longiflora* usually have a single interstitial chiasma makes the meiotic configuration (fig. 5, *c*) almost as distinctive of this species as is its somatic metaphase plate, both resulting from the uniformity in position of the subterminal insertion region.

In these four species the number of abortive grains present in mature pollen has been observed to vary at different seasons and under different growing conditions. In vigorous plants under favorable conditions the abortive grains form 4 to 10 per cent of the pollen. Under less favorable conditions they may constitute 10 to 25 per cent or, rarely, 40 per cent of the pollen grains, but do not approach the higher percentages observed in the hybrid plants (table 5).

CHROMOSOME BEHAVIOR IN F_1 HYBRIDS

All the six possible F_1 hybrids between *N. alata, N. bonariensis, N. Langsdorffii,* and *N. longiflora* have been grown, including reciprocal hybrids of *N. alata* × *N. Langsdorffii.* Many vigorous plants have been obtained of all these hybrids except *N. longiflora* × *N. bonariensis,* a cross from which only a single plant was obtained. This hybrid, after remaining in the rosette stage for a year, suggesting *N. bonariensis* in this respect, finally bloomed as a small weak plant, which was maintained for some time by cuttings. Its lack of vigor is in distinct contrast to the other hybrids, all of which showed good germination, viability, and normal longevity. All the hybrids were intermediate between the parental species in external morphological characters.

In contrast to the majority of interspecific hybrids of *Nicotiana,* a high degree of meiotic chromosome conjugation occurs in these F_1 hybrids with the exception of F_1 *N. longiflora* × *N. bonariensis.* Usually, *Nicotiana* species which are very similar in external and chromosome morphology show regular chromosome conjugation in their interspecific hybrids, and species dissimilar in these respects show various degrees of lack of conjugation. Multivalents have been observed in only a few hybrids (Goodspeed, 1934). In hybrids between species of the ALATA-GROUP, on the contrary, multivalents as well as bivalents occur, even where there is noticeable dissimilarity between the parents in external or chromosome morphology. The multivalents are of particular interest since, as has already been shown, certain definite morphological differences between the parental genoms can be identified (fig. 6). They have therefore received particular attention in this investigation and an attempt has been made to determine not only numbers, but also kinds of chromosomes in the multivalents.

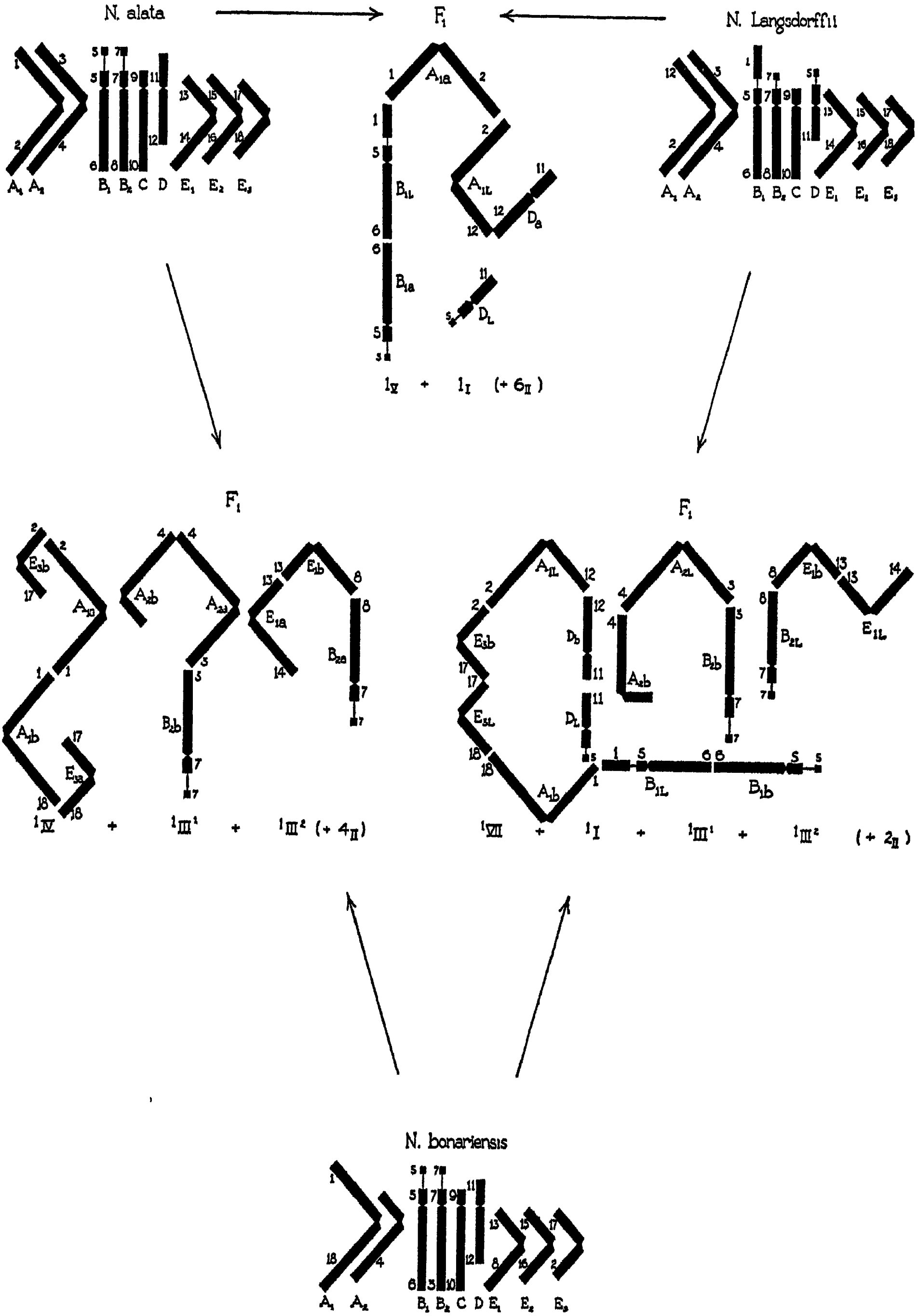

N. alata
F_1
N. Langsdorffii
A_1 A_2 B_1 B_2 C D E_1 E_2 E_3
A_{1a}
B_{1L}
B_{1a}
A_{1L}
D_a
D_L
1_V + 1_I (+ 6_{II})
F_1
E_{3b} A_{1a} A_{1b} E_{3a} A_{2b} A_{2a} B_{2b} E_{1b} E_{1a} B_{2a}
1_{IV} + $1_{III}{}^1$ + $1_{III}{}^2$ (+ 4_{II})
F_1
A_{1L} E_{3b} E_{3L} A_{1b} D_b D_L A_{2L} A_{2b} B_{2b} E_{1b} B_{2L} E_{1L} B_{1L} B_{1b}
1_{VII} + 1_I + $1_{III}{}^1$ + $1_{III}{}^2$ (+ 2_{II})
N. bonariensis

Fig. 6. Diagrammatic representation of the genoms of the 9-paired species and of the multivalent configurations in their F_1 hybrids. The subscript letters indicate the parental genom; e.g., $A_{1L} = A_1$ of *N. Langsdorffii.* The bivalents occurring but not shown are in parentheses.

F_1 *N. alata* × *N. Langsdorffii*

Brieger (1935) has pointed out that certain data on inheritance of characters in this hybrid cannot be accounted for on a strictly Mendelian basis, and suggests irregularities in chromosome conjugation as the reason. The evidence here presented confirms this interpretation. The recent genetic data of Smith (1937) likewise show significant deviations from ratios expected on chance distribution and recombination for two corolla color genes in the cross *N. Langsdorffii* × *N. Sanderae*. In the F_1 hybrid he observed that six chromosomes from each species pair to form normal bivalents, the remaining six chromosomes usually forming one quadrivalent and two univalents. He believes the genetic deviations may be due to the location of the genes concerned in chromosomes which do not pair to form bivalents.

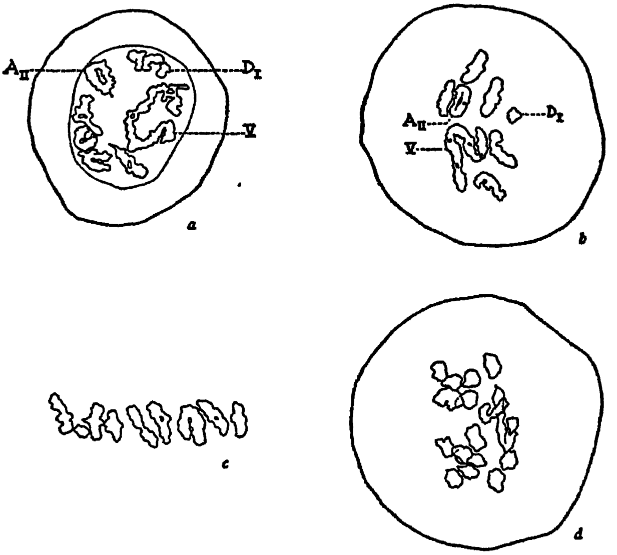


Fig. 7. PMC of F_1 *N. alata* × *N. Langsdorffii*. *a*, diakinesis, $1_V + 6_{II} + 1_I$; the quinquivalent, the ring bivalent of A chromosomes, and the unpaired D of *N. Langsdorffii* are labeled. *b*, early IM, $1_V + 6_{II} + 1_I$; the quiquivalent is presumed to consist of the following chromosomes from left to right: *N. alata* D, *N. Langsdorffii* A_I, *N. alata* A_I, *N. Langsdorffii* B_I, *N. alata* B_I; cf. figure 6. *c*, later IM, $1_{III} + 7_{II} + 1_I$, the units drawn in one plane. *d*, IA, 6 chromosomes at the upper and 8 at the lower pole, with 4 of the quinquivalent chromosomes lagging at the equator. × 1100.

The presence of three morphological distinctions between the somatic complements of *N. alata* and *N. Langsdorffii* suggests that the differentiation of these two species from a common ancestral form has involved chromosome reorganization, and correspondingly in F_1 meioses in place of nine bivalents the usual configuration is $1_V + 6_{II} + 1_I$ (cf. table 3 and fig. 7). Less frequently $1_{III} + 7_{II} + 1_I$ (fig. 7, *c*), $8_{II} + 2_I$ or 9_{II} occur. The formation of the quinquivalent indicates that at least two translocations must have been involved in the establishment in the two species of three chromosome pairs which differ in their organization. On the basis of size, it is possible to identify the three chromosomes of *N. Langsdorffii* which are involved. Thus, the very small univalent present at IM in the majority of PMC of the hybrid is the small satellited D chromosome of *N. Langsdorffii.* The quinquivalent (fig. 7, *a, b*) shows two terminal chromosomes which are smaller than the other three members of this association, and undoubtedly it is one of these two which is the *N. alata* homologue of the D chromosome of *N. Langsdorffii,* for the latter is sometimes

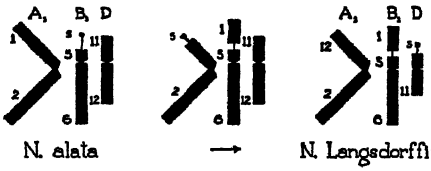
TABLE 3

FREQUENCY OF CONFIGURATIONS AT IM IN F_1 HYBRIDS OF 9-PAIRED SPECIES OF NICOTIANA

Configurations	F_1 hybrids			
	N. alata × *N. Langsdorffii*	*N. alata* × *N. bonariensis*	*N. Langsdorffii* × *N. bonariensis*	*N. Langsdorffii* × *N. bonariensis* (Müntzing, 1935)
9_{II}	5	..	..	..
$8_{\text{II}} + 2_{\text{I}}$	1	..	..	..
$1_{\text{III}} + 7_{\text{II}} + 1_{\text{I}}$	19	2	..	3
$1_{\text{VI}} + 6_{\text{II}}$	3	..	..	..
$1_{\text{V}} + 6_{\text{II}} + 1_{\text{I}}$	47	..	..	..
$1_{\text{IV}} + 6_{\text{II}} + 2_{\text{I}}$	..	2	..	..
$+ 2_{\text{III}} + 6_{\text{II}}$	..	3	..	3
$1_{\text{III}} + 6_{\text{II}} + 3_{\text{I}}$	..	..	2	..
$2_{\text{IV}} + 5_{\text{II}}$	..	2	..	..
$1_{\text{IV}} + 1_{\text{III}} + 5_{\text{II}} + 1_{\text{I}}$	..	20	..	..
$2_{\text{III}} + 5_{\text{II}} + 2_{\text{I}}$	..	4	4	4
$1_{\text{IV}} + 2_{\text{III}} + 4_{\text{II}}$	..	9	1	1
$1_{\text{IV}} + 1_{\text{III}} + 4_{\text{II}} + 3_{\text{I}}$	..	5	..	..
$3_{\text{III}} + 4_{\text{II}} + 1_{\text{I}}$	..	2	6	9
$4_{\text{III}} + 3_{\text{II}}$	..	..	..	1
$1_{\text{IV}} + 2_{\text{III}} + 3_{\text{II}} + 2_{\text{I}}$	..	1	3	..
$3_{\text{III}} + 3_{\text{II}} + 3_{\text{I}}$	..	..	4	1
$1_{\text{VII}} + 2_{\text{III}} + 2_{\text{II}} + 1_{\text{I}}$	..	..	1	..
$4_{\text{III}} + 2_{\text{II}} + 2_{\text{I}}$	..	..	4	1
Total................	75	50	25	23

conjugated with the quinquivalent to form a sexavalent. Two of the three larger chromosomes in the quinquivalent are A chromosomes since they are the largest chromosomes present at IM of the F_1. One large ring bivalent occurs among the six pairs formed in addition to the quinquivalent and univalent (fig. 7, *a, b*), and as such a configuration is characteristic of the A chromosomes in both species, this bivalent must be composed of the two A chromosomes not present in the quinquivalent. The other large chromosome of the quinquivalent is probably the large satellited B_1 member of the *N. Langsdorffii* genom since it is the only chromosome of large size in the parental complements which has not already been accounted for. The final member of the quinquivalent is, then, presumably the *N. alata* homologue of this large satellited B_1 chromosome of *N. Langsdorffii.* It is probable but not certain that this is one of the satellited B chromosomes of *N. alata* and that it forms the terminal chromosome of the quinquivalent at the end opposite to the *N. alata* D chromosome. Accordingly, we have in the quinquivalent a B_1 chromosome from *N. alata,* the large satellited B_1 chromosome from *N. Langsdorffii,* two A_1 chromosomes (one from *N. alata* and one from *N. Langsdorffii*), and, finally, the D chromosome from *N. alata* (figs. 6; 7, *a, b*).

It is possible that the differentiation of these two species from each other has involved the establishment of two successive reciprocal translocations between the chromosomes assumed to be present in the quinquivalent, as suggested in the following diagram.



The observed distinctions in chromosome organization in the two species might have arisen at one time if the three chromosomes were simultaneously involved in the manner which Dubinin and Khvostova (1935) have shown to be characteristic of radiation-induced reorganizations. Whatever the mode of origin of the differences in organization, they account for the formation of the quinquivalent in the hybrid and the morphological differences between the genoms of *N. alata* and *N. Langsdorffii,* as is shown in figure 6.

Although multivalent formation is characteristic of the three different populations of this hybrid studied, it does not cause great irregularity in IA distribution. Usually the quinquivalent is oriented so that it will disjoin to give three chromosomes at one pole and two at the other. When the three

TABLE 4

DISTRIBUTION OF CHROMOSOMES AT IIM IN THE F_1 HYBRIDS OF 9-PAIRED SPECIES

Hybrids	IIM distribution						Frag-ments	Total
	$\frac{9}{9}$	$\frac{8}{10}$	$\frac{7}{11}$	$\frac{8}{9}-1$	$\frac{8}{8}-2$	$\frac{7}{10}-1$		
1. *N. alata* × *N. Langsdorffii* and reciprocal	45	17	....	15	....	....	7	84
Per cent	53.6	20.2	....	17.9	....	....	8.3	100
2. *N. alata* × *N. bonariensis*	5	4	1	9	2	....	4	25
Per cent	20	16	4	36	8	....	16	100
3. *N. Langsdorffii* × *N. bonariensis*[a]	7	7	3	10	....	2	[b]	29
Per cent	24.1	24.1	10.3	34.5	....	6.9	....	99.9

[a] Quoted from Müntzing, 1935.

[b] PMC containing fragments not included in this count.

chromosomes of the quinquivalent go to one pole and the univalent goes to the other, a normal 9–9 distribution will result. Such a distribution was observed at IIM in 54 per cent of PMC of four different F_1 plants in which all chromosomes could be counted (table 4). However, the various orientations assumed by the quinquivalent indicate that a 3–2 distribution will not always send the same three chromosomes to one pole. Some of these distributions, although numerically normal, probably result in the formation of inviable pollen grains, as indicated by the occurrence of 10 per cent less (44 per cent) of good stainable pollen grains (cf. table 5) than of 9–9 distributions at IIM (54 per cent).

TABLE 5

SPORAD AND POLLEN COUNTS IN F_1 HYBRIDS OF 9-PAIRED SPECIES

Hybrids	Number of cells in sporads					Pollen		
	4	5	6	Total	Per cent ab-normal	Total no. of grains	Stained	Unstained
N. alata × *N. Langsdorffii* and reciprocal	164	34	2	200	....	941	412	529
Per cent	82	17	1	100	18	....	43.8	56.2
N. alata × *N. bonariensis*	183	65	2	250	....	1191	164	1027
Per cent	73 2	26	0.8	100	26.8	....	13.8	86.2
N. Langsdorffii × *N. bonariensis*	116	77	7	200	....	....	....	......
Per cent	58	38.5	3.5	100	42	....	....	......
Müntzing, 1935								
Per cent	55	41	4	100	45	....	18	82

The univalent went to the pole along with the three chromosomes of the quinquivalent in 20 per cent of PMC, and lagged between the poles in 18 per cent. Furthermore, divided or fragmented chromosomes were present in 8 per cent of the PMC at IIM. Often the quinquivalent was late in disjunction (fig. 7, *d*), but usually its members were included in the telophase nuclei. The number of microcytes at the sporad[8] stage corresponds closely to the number of PMC with lagging chromosomes, 18 per cent having one or two micronuclei (table 5). The 44 per cent of good pollen characteristic of this hybrid is sufficient to produce viable seed on selfing.

F_1 *N. alata* × *N. bonariensis*

We have seen that *N. alata* and *N. Langsdorffii* exhibit many differences in external morphology and a few distinctions between their genoms which, if originating in chromosome reorganizations in ancestral stocks, would account for the formation of the quinquivalent observed in their F_1 hybrid. In *N. alata* and *N. bonariensis,* however, another relationship exists between these three independent evidences of differentiation, for the two species are more similar in both external and chromosome morphology than are *N. alata* and *N. Langsdorffii;* but the amount of multivalent formation in their F_1 hybrid is much increased over that in F_1 *N. alata* × *N. Langsdorffii.* Thus, nine bivalents were never observed and one, two, or three multivalents are formed. The most frequent configuration (40 per cent of PMC; cf. table 3) is $1_{\mathrm{IV}} + 1_{\mathrm{III}} + 5_{\mathrm{II}} + 1_{\mathrm{I}}$ (fig. 8, *a, b*). However, two trivalents in addition to a quadrivalent often occur (18 per cent of PMC) and this configuration ($1_{\mathrm{IV}} + 2_{\mathrm{III}} + 4_{\mathrm{II}}$; fig. 8, *c, d*) is probably the basic one, exhibiting the fundamental chromosome homologies. Nearly all other observed configurations (28 per cent of PMC) are variations of it which involve increased incidence of univalents, that is, $1_{\mathrm{IV}} + 1_{\mathrm{III}} + 4_{\mathrm{II}} + 3_{\mathrm{I}}$ (fig. 8, *e*); $3_{\mathrm{III}} + 4_{\mathrm{II}} + 1_{\mathrm{I}}$ (fig. 8, *f*); $2_{\mathrm{III}} + 5_{\mathrm{II}} + 2_{\mathrm{I}}$ (fig. 8, *g*); $1_{\mathrm{IV}} + 2_{\mathrm{III}} + 3_{\mathrm{II}} + 2_{\mathrm{I}}$; $1_{\mathrm{IV}} + 6_{\mathrm{II}} + 2_{\mathrm{I}}$. Other configurations (14 per cent of PMC) include the formation of two bivalents instead of a quadrivalent, or, rarely, the formation of two quadrivalents—$1_{\mathrm{III}} + 7_{\mathrm{II}} + 1_{\mathrm{I}}$ (fig. 8, *h*); $2_{\mathrm{III}} + 6_{\mathrm{II}}$; $2_{\mathrm{IV}} + 5_{\mathrm{II}}$.

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[8] Sporad = group of microspores resulting from the meiotic divisions of a single PMC; inclusive term for monad, dyad, triad, tetrad, etc.; cf. Webber, 1933.

In order to analyze the constitution of the multivalent configurations in terms of the chromosome morphologies of the parental genoms, the multivalents in 16 PMC where $1_{\mathrm{IV}} + 1_{\mathrm{III}} + 5_{\mathrm{II}} + 1_{\mathrm{I}}$ occurred were drawn and compared. The same chromosomes were always involved in the quadrivalent, the two central ones being large and the two terminal ones smaller. In 13 of the 16 PMC a normal distribution of chromosomes would have resulted from the orientation of the quadrivalent at metaphase, one of the large and one of the smaller chromosomes going to each pole. In 3, the two smaller chromosomes were directed toward one pole, and the two larger to the other, and in 2 of these 3 a ring quadrivalent had been formed, owing to chiasma formation between the two smaller chromosomes. The two large chromosomes in the quadrivalent are undoubtedly A chromosomes present in both parental species. Three terminal chiasmata occur in the quadrivalent at metaphase, the two A chromosomes having a chiasma in each arm, and the smaller chromosomes forming a chiasma in one arm only.

The trivalent accompanying the quadrivalent may show more variation than the latter in its configuration. Thus, three larger chromosomes were involved in the trivalent in 7 of the 16 PMC, and in 5 of these one chiasma was interstitial and one terminal by metaphase, giving it a characteristic " + " configuration. In 2 all chiasmata were terminal at metaphase. Although all the chromosomes in this trivalent are not of the same size, there are not such distinct size differences as occur in the quadrivalent. Often one of the two short arms at the unterminalized chiasma was longer than the other (fig. 8, *c*), indicating that the chromosomes were heteromorphic. This trivalent of larger chromosomes will be designated III^1. In 9 of the 16 PMC a trivalent of medium-sized chromosomes occurred, in which the two chiasmata were always completely terminalized by metaphase to give it a "V" shape. The two terminal chromosomes of this trivalent were usually oriented toward the same pole, the middle chromosome, with a median insertion region, being directed toward the op-

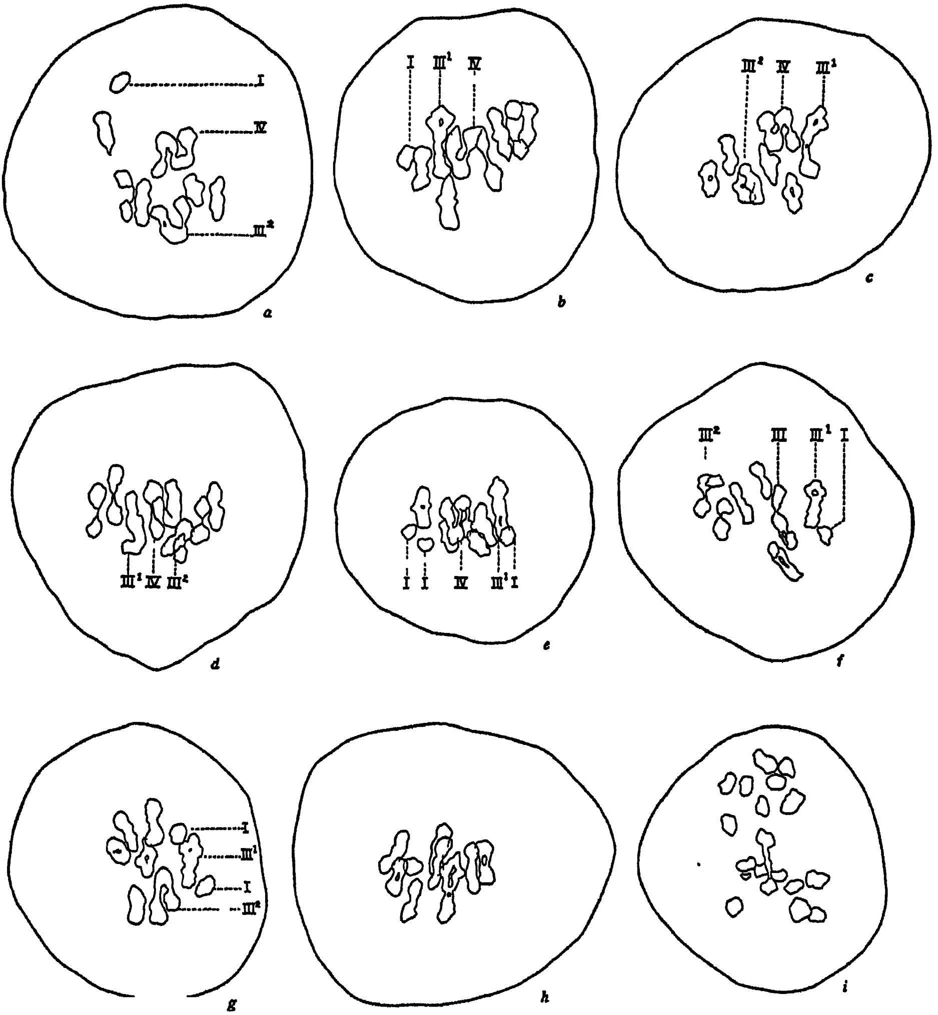

Fig. 8. PMC of F$_1$ *N. alata* × *N. bonariensis*. *a–h*, IM: *a*, $1_{IV} + 1_{III}^{2} + 5_{II} + 1_{I}$; *b*, $1_{IV} + 1_{III}^{1} + 5_{II} + 1_{I}$; *c*, *d*, $1_{IV} + 1_{III}^{1} + 1_{III}^{2} + 4_{II}$; *e*, $1_{IV} + 1_{III}^{1} + 4_{II} + 3_{I}$; *f*, $3_{III} + 4_{II} + 1_{I}$; *g*, $2_{III} + 5_{II} + 2_{I}$; *h*, $1_{III} + 7_{II} + 1_{I}$; *i*, IA, 8 chromosomes at each pole, with one bivalent and a fragment lagging in the equatorial region. × 1300.

posite pole. In at least 3, it appeared that a chiasma had been formed between the two terminal chromosomes. The designation III^2 will be used for this trivalent.

These two types of configuration found in PMC with one trivalent both occurred in a single PMC where two trivalents were formed in addition to the quadrivalent. Where three trivalents occurred, all three were different, one being of the III^1 and one of the III^2 type, and the third, consisting of two larger chromosomes and a smaller one, apparently corresponded to three of the four chromosomes in the quadrivalent (fig. 8, *f*).

The analysis of these types of chromosome conjugation indicates that the difference in genic organization between *N. alata* and *N. bonariensis* involves at least five pairs of chromosomes. The two large A pairs characteristic of both species are concerned, one having to do with quadrivalent formation and one with the formation of III^1. This is clear because one never finds in F$_1$ *N. alata* × *N. bonariensis,* when maximum conjugation occurs, the large ring bivalents characteristic of the A$_1$ and A$_2$ chromosomes in the parental species and of the one A pair in F$_1$ *N. alata* × *N. Langsdorffii.* One ring bivalent has been observed when III^1 was not formed. It therefore seems probable that the quadrivalent involves two A chromosomes, one from each of the two species, and two chromosomes of shorter length, possibly the shortest of the E pairs in each species. If so, the two A chromosomes concerned, although morphologically similar, are genetically different, and likewise the two E.

The III^1 involves an A chromosome of *N. alata,* as judged by size, and its *N. bonariensis* homologue, which is probably the J-shaped A$_2$ chromosome since it is smaller than the *N. alata* A. The third chromosome in this trivalent usually possesses a single terminalized chiasma by metaphase and, therefore, probably represents a satellited B chromosome of *N. bonariensis.* In the III^2 with three medium-sized chromosomes, the middle chromosome regularly forms a chiasma in each arm and is undoubtedly a chromosome with a median insertion region. Since it is not large enough to be an A chromosome it is probably the largest of the E chromosomes of *N. bonariensis,* one of the other chromosomes being its homologue in *N. alata.* The fact that all chromosomes are conjugated when $1_{\mathrm{IV}} + 2_{\mathrm{III}} + 4_{\mathrm{II}}$ are formed means that the homologue of one of the chromosomes involved in III^1 must also be involved in III^2, and this is probably an *N. alata* B chromosome.

In the analysis of the multivalents represented diagrammatically in figure 6, the somatic chromosomes presumed to be concerned have been arranged in characteristic configurations. The differences in numbering of chromosome ends in the three species are the fewest possible to account for the multivalents observed and it is probable that the actual number of differences in chromosome organization exceed the number accounted for in the diagram. Even if some of the chromosomes involved have been wrongly identified from lack of definition in meiotic configurations, the minimum number of reorganizations necessary to account for the chromosome behavior in the hybrids is as represented in this diagram.

The distribution at IA following the higher frequency of multivalent formation at IM is more irregular in this hybrid than in F$_1$ *N. alata* × *N. Langsdorffii,* as evidenced by the IIM counts in PMC where all chromosomes could be identified. Thus, 20 per cent (cf. table 4) of the PMC showed a 9–9 distribution, 16 per cent a 10–8, 36 per cent a 9–1–8, 4 per cent an 11–7, 8 per cent an 8–2–8, and 16 per cent fragmented or divided chromosomes. Chromatin bridges with small fragments near by were occasionally seen at IA (fig. 8, *i*), indicating that here, as in the F$_1$ *N. Langsdorffii* × *N. bonariensis* hybrid described by Müntzing (1935), crossing over may occur between nonaligned insertion regions of conjugating chromosomes, giving rise both to fragments and to chromosomes with two insertion regions.

The amount of good pollen formed is less than the number of IIM's with a 9–9 distribution, presumably as a result of a qualitatively dissimilar chromosome distribution. As already mentioned, a similar situation obtains in F_1 *N. alata* × *N. Langsdorffii,* and the amount of the reduction is approximately the same in the two hybrids, that is, in F_1 *N. alata* × *N. Langsdorffii* from 54 to 44 per cent and in F_1 *N. alata* × *N. bonariensis* from 20 to 14 per cent (tables 4 and 5). The number of microcytes in the sporads is higher in F_1 *N. alata* × *N. bonariensis,* 26.8 per cent having one, or rarely two, microcytes (table 5). Several plants have produced selfed seed whose viability has not yet been tested, but no seed has been obtained from crosses with the parental species.

F_1 *N. Langsdorffii* × *N. bonariensis*

Having obtained some index to degree of differentiation in genic organization between the chromosome complements of *N. alata* and those of *N. bonariensis* and *N. Langsdorffii,* it is of interest to see whether an analysis of the pairing relations in F_1 *N. Langsdorffii* × *N. bonariensis* bears out the conclusions reached in the study of the other two hybrids. We have assumed that two successive reciprocal translocations involving the A_1 chromosome of *N. Langsdorffii* have given rise to the visible differences between the *N. alata* and *N. Langsdorffii* genoms. We have assumed also that three reciprocal translocations, only one of which involved the same chromosome pair as was concerned in the *alata-Langsdorffii* translocations, differentiate the *N. bonariensis* genom from that of *N. alata.* When, then, we combine the *N. Langsdorffii* and the *N. bonariensis* complements, these five differences should be manifested in the type of chromosome conjugation which occurs. If we combine the translocations which best account for the size and configurations of chromosomes observed in the two hybrids already discussed, we find that it gives a possible association between the complements of *N. Langsdorffii* and *N. bonariensis* of $1_{VIII} + 2_{III} + 2_{II}$, or, if the *N. Langsdorffi* D chromosome fails to form a chiasma, of $1_{VII} + 2_{III} + 2_{II} + 1_{I}$. Although this latter configuration was observed only once in the hybrid between these species (cf. fig. 9, *a*), two bivalents were found to be the minimum number formed in 16 per cent of the IM's studied (table 3), these being accompanied by $4_{III} + 2_{I}$ (fig. 9, *b* and *c*). This type of conjugation can be accounted for if the chiasma frequency in certain of the chromosomes involved is too low to insure the formation of units larger than quadrivalents or trivalents. According to this interpretation of chromosome behavior in this hybrid, many different types of chromosome conjugation are to be expected. Although only a limited number of PMC were studied, many variations in configuration were seen. The observations of Müntzing (1935), who has studied this hybrid, correspond to those recorded in table 3, and have been used to supplement them. The configurations $1_{VII} + 2_{III} + 2_{II} + 1_{I}$ (fig. 9, *a*), $1_{IV} + 2_{III} + 3_{II} + 2_{I}$, and $1_{III} + 6_{II} + 3_{I}$ recorded here were not reported by Müntzing, and an equal number of configurations not reported here were observed by Müntzing, namely, $1_{III} + 7_{II} + 1_{I}$, $2_{III} + 6_{II}$, and $4_{III} + 3_{II}$. All these different configurations can be interpreted on the basis of the assumed homologies of the chromosomes of *N. bonariensis* and *N. Langsdorffii*, and correspond to expectation on the basis of the sizes and insertion regions of the chromosomes involved. Thus, the chromosome which might be expected to be unpaired is the *N. Langsdorffii* D, which corresponds in size to the unpaired chromosome observed and figured at IM by Müntzing as well as in the hybrid reported here (fig. 9). The association of a terminal member of a trivalent of larger chromosomes with the nucleolus (fig. 9, *f*) indicating that it is a satellited B chromosome is also to be noted, because this trivalent corresponds in its size and behavior to the expected one composed of the *N. bonariensis* A_2,

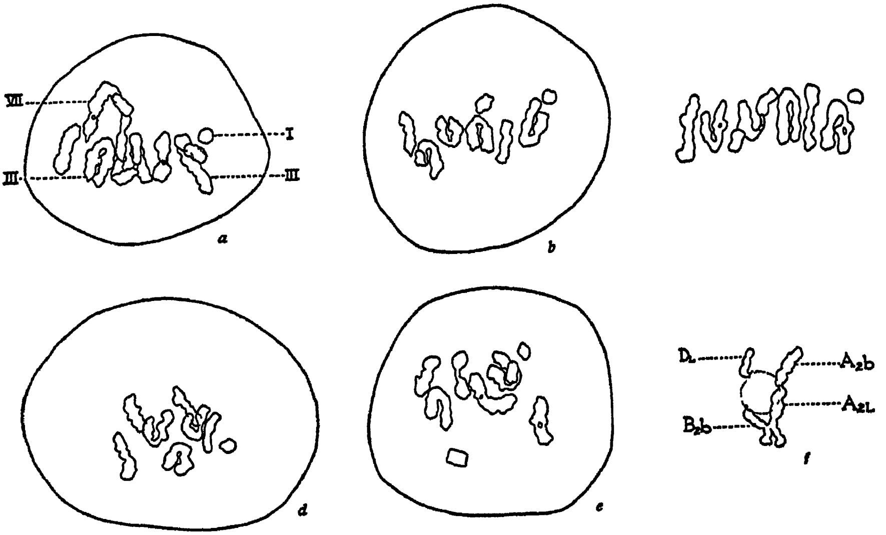

Fig. 9. PMC of F_1 *N. Langsdorffii* × *N. bonariensis*. *a–e*, IM: *a*, $1_{VII} + 2_{III} + 2_{II} + 1_{I}$; *b*, *c*, $4_{III} + 2_{II} + 2_{I}$; *d*, $3_{III} + 4_{II} + 1_{I}$; *e*, $3_{III} + 3_{II} + 3_{I}$; *f*, diakinesis, one trivalent and one univalent associated with the nucleolus (cf. figure 6). × 1133.

the *N. Langsdorffii* A_2, and the *N. bonariensis* B_2 (cf. fig. 6). The correspondence between expected and observed configurations is thus close, and leads to the conclusion that the differences in genic organization between the three 9-paired species are the product of relatively few chromosomal alterations.

The distribution of chromosomes at IIM was not studied statistically in this hybrid, but as counts of configurations at IM and of sporads agree closely with those of Müntzing (1935), his record of IIM distribution may be considered typical (table 4). He found that in this hybrid as in F_1 *N. alata* × *N. bonariensis* the most frequent distribution was 8–1–9, forming 34.5 per cent PMC in which no fragments occurred. The distributions 9–9 and 8–10 were equally frequent (24.1 per cent), and 7-11 and 7-1-10 were infrequent (10.3 per cent and 6.9 per cent, respectively). At the sporad stage he reported 55 per cent with four cells, 41 per cent with five cells, and 4 per cent with six cells. This is very similar to the sporad count of the hybrid studied in the present investigation (table 5), where 200 PMC gave 58 per cent with four cells, 38.5 per cent with five cells, and 3.5 per cent with six cells. Müntzing counted 18 per cent good pollen grains in his hybrid (table 5), a slightly higher percentage than that in F_1 *N. alata* × *N. bonariensis* (14 per cent), but lower than that in F_1 *N. alata* × *N. Langsdorffii* (44 per cent). R. E. Clausen (unpublished) has been able to obtain some seed from this hybrid in backcrosses, but its viability has not as yet been tested.

THE F_1 HYBRIDS BETWEEN *N. longiflora* AND THE 9-PAIRED SPECIES

It has already been pointed out that in many morphological details *N. longiflora* is similar to the 9-paired species, especially to *N. alata*, and yet has a chromosome complement which is distinct from these species in respect to both number and morphology. A question thus arises concerning the extent to which the chromosomes of *N. longiflora* and of the 9-paired group give evidence of a common genic substratum as determined by meiotic chromosome behavior in their F_1 hybrids. The three hybrids of *N. longiflora* with *N. alata*, *N. Langsdorffii*, and *N. bonariensis* have been obtained, the first two being vigorous, intermediate between the parental species in morphological characters, and sterile, and the last being represented by a single weak plant which was again intermediate in morphological characters and sterile.

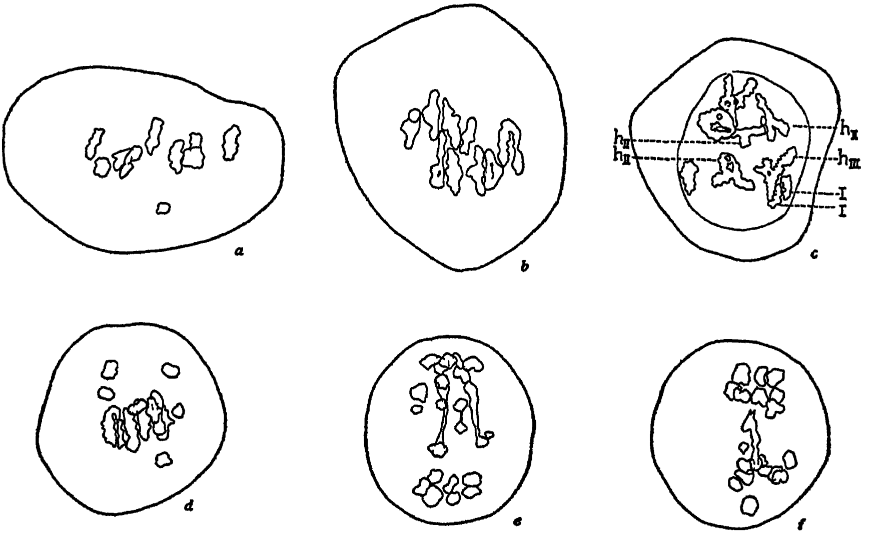

Fig. 10. PMC of F_1 *N. longiflora* × *N. alata*. *a, b*, IM: *a*, $9_{II} + 1_{I}$; *b*, $1_{III} + 8_{II}$; *c*, diakinesis, $1_{III} + 7_{II} + 2_{I}$ (h_{II} = heteromorphic bivalent; h_{III} = heteromorphic trivalent); *d*, IM, $1_{III} + 5_{II} + 6_{I}$; *e, f*, IA, chromosomes with two insertion regions and fragments lagging in the equatorial region. × 1100.

The most frequent chromosome configuration at IM of PMC in F_1 *N. longiflora* × *N. alata* is $9_{II} + 1_{I}$ (fig. 10, *a*), which suggests that all the *N. alata* chromosomes have paired with 9 of the 10 *N. longiflora* chromosomes, leaving one *N. longiflora* chromosome unpaired. With almost the same frequency (table 6) as the configuration just given, $1_{III} + 8_{II}$ occurs (fig. 10, *b*). It is clear, however, that the chromosomes of the two complements are not exactly alike in their organization, for the conjugating chromosomes are frequently not of the same length or morphology. At least three pairs are heteromorphic at diakinesis and IM (fig. 10, *b, c*). Other configurations observed can be interpreted in terms of these two most frequent ones, accompanied by increased nonconjunction in certain pairs. Thus, $1_{\rm III} + 7_{\rm II} + 2_{\rm I}$ (fig. 10, *c*) and $8_{\rm II} + 3_{\rm I}$ are of relatively frequent occurrence, whereas $1_{\rm III} + 6_{\rm II} + 4_{\rm I}$, $7_{\rm II} + 5_{\rm I}$, $1_{\rm III} + 5_{\rm II} + 6_{\rm I}$ (fig. 10, *d*), and $6_{\rm II} + 7_{\rm I}$ are of rare occurrence (cf. table 6).

TABLE 6

FREQUENCY OF CONFIGURATIONS AT IM IN F_1 HYBRIDS BETWEEN 9- AND 10-PAIRED SPECIES OF NICOTIANA

Configurations	F_1 hybrids		
	N. longiflora × *N. alata*	*N. longiflora* × *N. Langsdorffii*	*N. longiflora* × *N. bonariensis*
$9_{\rm II} + 1_{\rm I}$	17	46	..
$1_{\rm III} + 8_{\rm II}$	14	3	..
$8_{\rm II} + 3_{\rm I}$	5	27	..
$1_{\rm III} + 7_{\rm II} + 2_{\rm I}$	9	11	..
$7_{\rm II} + 5_{\rm I}$	1	5	..
$2_{\rm III} + 6_{\rm II} + 1_{\rm I}$	1	2	..
$1_{\rm III} + 6_{\rm II} + 4_{\rm I}$	2	..	..
$6_{\rm II} + 7_{\rm I}$	1	1	..
$2_{\rm III} + 5_{\rm II} + 3_{\rm I}$	..	1	..
$1_{\rm III} + 5_{\rm II} + 6_{\rm I}$	2	..	..
$3_{\rm II} + 13_{\rm I}$	..	..	4
$2_{\rm II} + 15_{\rm I}$	..	..	11
$1_{\rm II} + 17_{\rm I}$	..	..	35
$0_{\rm II} + 19_{\rm I}$	..	..	28
Total........................	52	96	78

At the meiotic anaphase in this hybrid, chromatin bridges are of rather frequent occurrence and usually a count of all units present shows that these bridges are formed by two chromosomes which have failed to disjoin (fig. 10, *e, f*). In many such occurrences the lagging chromosomes are accompanied by small fragments, and are chromosomes with two insertion regions which, presumably, have resulted from crossing over between morphologically unlike chromosomes whose insertion regions were not aligned at pachytene. These chromatin bridges, together with the heteromorphic bivalents at diakinesis, are evidence that conjugation of morphologically dissimilar chromosomes has occurred.

The hybrid between *N. longiflora* and *N. Langsdorffii* shows configurations similar to those of F_1 *N. longiflora* × *N. alata,* but a few PMC with increased trivalent formation, $2_{\rm III} + 6_{\rm II} + 1_{\rm I}$ and $2_{\rm III} + 5_{\rm II} + 3_{\rm I}$, were observed. The most frequent configuration was $9_{\rm II} + 1_{\rm I}$, next $8_{\rm II} + 3_{\rm I}$ (fig. 11, *a*), followed by $1_{\rm III} + 7_{\rm II} + 2_{\rm I}$ (fig. 11, *b, c*), $1_{\rm III} + 8_{\rm II}$ (fig. 11, *d–f*), and $7_{\rm II} + 5_{\rm I}$ (cf. table 6). In this hybrid heteromorphic pairs were conspicuous at diakinesis. Thus, in figure 11, *b*, nearly all bivalents and the trivalent are composed of chromosomes of dissimilar length or insertion region, and the same is true of at least five of the nine configurations in figure 11, *d* and *e*. Even after the increased contraction at IM, size differences are apparent not only in the bivalents, but also in the univalent chromosomes, which are seen to be conjugated to form bivalents or trivalents in other PMC. For example, when $8_{II} + 3_I$ occurs, the three univalents are of three different sizes, one very large, one slightly smaller, and one very small (fig. 11, *a*).

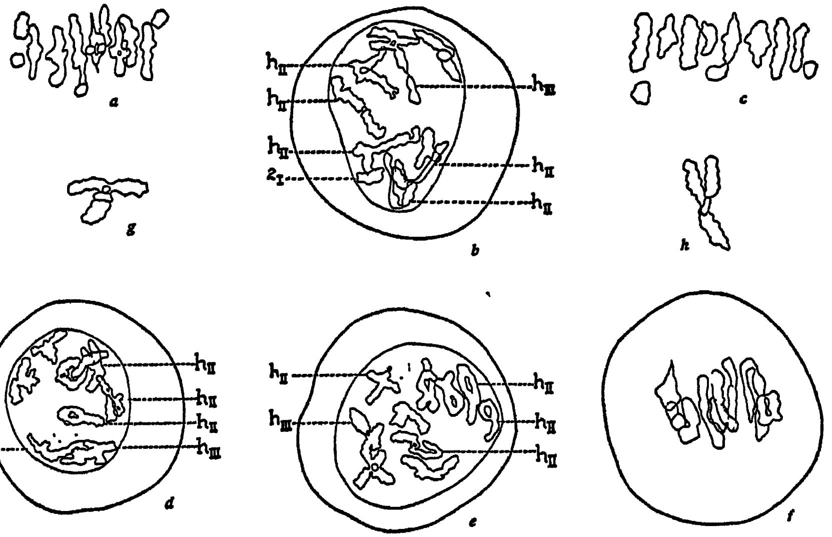

Fig. 11. PMC of F_1 *N. longiflora* × *N. Langsdorffii.* *a*, IM, $8_{II} + 3_I$; *b*, diakinesis, $1_{III} + 7_{II} + 2_I$, five heteromorphic bivalents, a trivalent, and two univalents being labeled; *c*, IM, $1_{III} + 7_{II} + 2_I$, showing difference in size of univalents; *d*, *e*, diakinesis, $1_{III} + 8_{II}$, four heteromorphic bivalents and one trivalent indicated in each PMC; *f*, IM, $1_{III} + 8_{II}$; *g*, *h*, heteromorphic bivalents at diakinesis, showing trivalent-like configuration. *a–f*, × 1133; *g–h*, × 1650.

The heteromorphic pairs are of particular interest, and deserve further consideration. The components of these bivalents, one longer and one shorter, differ in length from a barely perceptible extent to one-fourth, one-half, or the total length of the smaller one. At diakinesis and IM, various configurations formed by these heteromorphic bivalents may be seen. Thus, if they contain a single chiasma, "×'s" and "+'s" with unequal arms will appear at diakinesis. A large bivalent composed of one very large and one small chromosome, the latter approximately one-half the length of the former, is often seen to be held together by two chiasmata, one at or near each end of the smaller chromosome, thus giving rise to a "frying pan" configuration similar to that characteristic of certain trivalents (fig. 11, *d*, *e*). If only a single chiasma is formed, it is frequently localized in the median region of the longer chromosome, apparently because it is formed between the insertion regions of the two chromosomes. It was not determined whether the two insertion regions were separated by the length of the long or the short arm of the shorter chromosome, but, whichever it was, the single localized chiasma produced gives a conspicuous "Y" configuration to this bivalent (fig. 11, *g, h*). From size relations and the regular conjugation of these chromosomes it appears that a large A chromosome of *N. Langsdorffii* is homologous with a shorter chromosome of *N. longiflora.* The fact that these two chromosomes are always so conjugated that two of their ends are together and that these ends may be joined by a chiasma while the other end of the shorter chromosome also may form a chiasma with the median region of the longer chromosome, suggests that the *N. longiflora* chromosome concerned must be genically similar throughout the major part of its length to approximately one-half of an *N. Langsdorffii* A chromosome.

As in F_1 *N. longiflora* × *N. alata,* a single trivalent occurs rather frequently in this hybrid. It may consist either of two larger and one smaller chromosome, or of two smaller and one larger chromosome. This latter configuration was well shown at diakinesis, where the exchange of chromatids could be followed at each of the chiasmata (fig. 11, *e*). In this diakinesis a single large *N. Langsdorffii* chromosome has conjugated with two smaller chromosomes, presumably both from *N. longiflora.*

The regular conjugation of the chromosomes of these two 9-paired species with those of the 10-paired species, together with the fact that equivalent conjugation does not occur in hybrids between them and species outside the ALATA-GROUP, suggests that the complements involved have been derived from a common stock. The distinction in chromosome number could have involved either fusion of two chromosomes with subterminal insertion regions in a 10-paired race to give nine pairs, or fragmentation of a large medianly constricted chromosome of a 9-paired race to give ten pairs. Such alteration would account only for the difference in chromosome number and in the morphology of one pair of chromosomes of the two species. An accumulation of translocations could account for the other distinctions between the species involved, such as the five chromosome pairs in *N. Langsdorffii* and *N. alata* which differ from *N. longiflora* chromosomes in having median insertion regions. Factors which may have aided in the establishment of these extensive structural changes in the chromosomes and the direction in which such changes appear to have proceeded will be discussed below. Here it should be pointed out again that regularity of chromosome conjugation with large differences in the structure of the conjugating chromosomes characterizes these two hybrids between the 9- and 10-paired species.

Chromosome behavior in the third hybrid between 9- and 10-paired species, *N. longiflora* × *N. bonariensis,* is in distinct contrast to that of the other hybrids just discussed, for here very little chromosome conjugation occurs. Since in the other hybrids the expectation based on observed behavior has been reasonably fulfilled, one must suspect that some physiological, environmental, or genetic factor may have been operating here to reduce the chromosome pairing. Additional hybrids must be studied, therefore, to determine whether or not the chromosome behavior in this hybrid plant is typical of the F_1. An

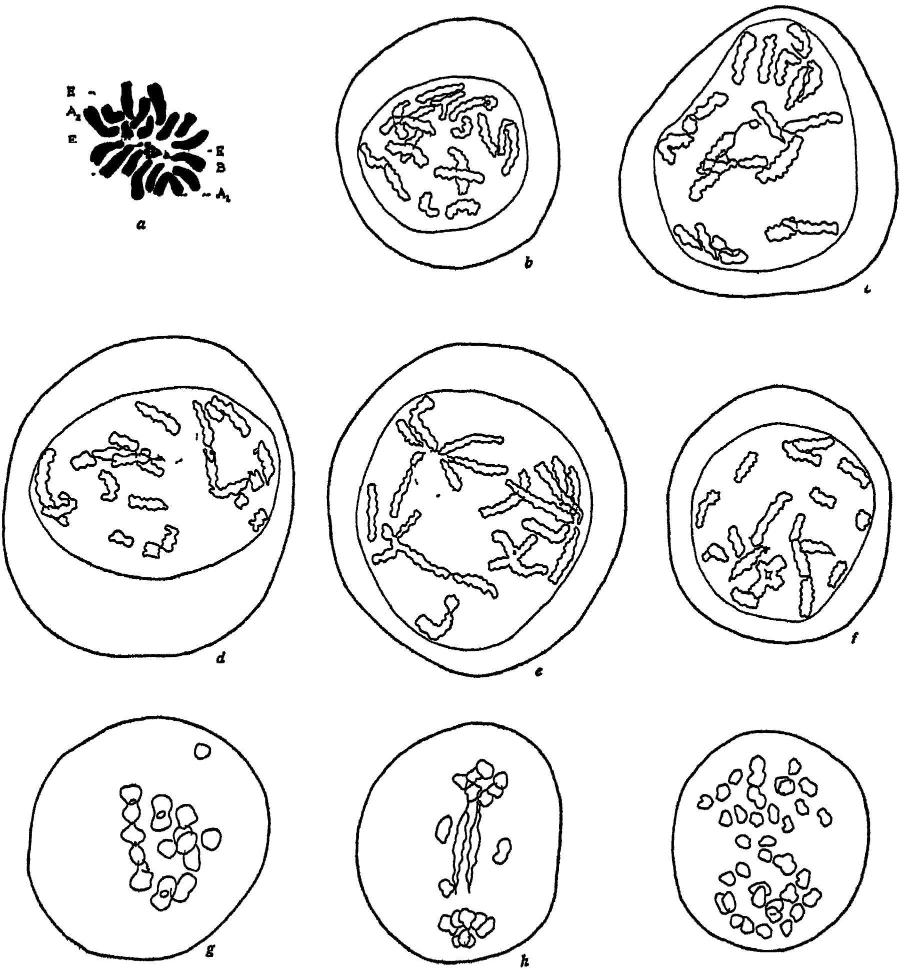

Fig. 12. F_1 *N. longiflora* × *N. bonariensis*. *a*, metaphase of mitosis in anther wall, 19 chromosomes, 7 of which can be identified as chromosomes of *N. bonariensis*. *b–i*, PMC: *b–f*, diakinesis; *b*, *c*, 19_I, chromosomes in *c* showing separation of arms at the insertion regions; *d*, 21 units, some of which are fragments; *e*, $2_{II} + 15_I$, the apparent trivalent in the lower center probably representing separation of a large chromosome of a bivalent at its insertion region; *f*, $1_{II} + 17_I$; *g*, IM, $3_{II} + 13_I$; *h*, IA, 5 chromosomes lagging in the equatorial region; *i*, early IIM, 19 chromosomes in each plate, of which 2 in the upper and 4 in the lower have not yet completely separated from the previous equational division. × 1300.

account of its meiotic behavior will be given at this time because of its cytological interest.

That the single plant available possessed a typical somatic chromosome complement was determined by study of a metaphase plate found in an anther wall cell (fig. 12, *a*). At diakinesis all the nineteen chromosomes could sometimes be identified, distributed about the nucleus (fig. 12, *b*), but usually many of them appeared to be separating into two distinct parts at the insertion region with the result that the proximal portion took on the appearance of a satellite or attached fragment (fig. 12, *c*). In such PMC it was often possible to interpret all the chromosomes present; in many others (fig. 12, *d*) the number of units was so much increased that interpretation in terms of the original nineteen chromosomes was impossible. The PMC studied, although often much flattened, were not visibly injured by smearing; hence the apparent fragmentation cannot be ascribed to the technique used. It is possible that precocious division of certain chromosomes occurs, but this would not account for the typical picture in which small fragments are being separated from large chromosomes (fig. 12, *c, d*). Presumably the variety and number of units observed are related to chromosome breakage, which begins early in meiosis at primary, secondary (satellites), or tertiary constrictions (Lewitsky, 1931*a*).

The difficulties of interpretation of units is increased by the fact that entire chromosomes may stick together to form chains of two to six or more. This behavior is found in haploid plants (Lammerts, 1934) and hybrids between distantly related species of *Nicotiana*. In figure 12, *g*, besides three bivalents, six chromosomes are held together by tenuous connections to form a chain. Lammerts (1934) has called such attachments "off-spindle associations," and these probably account for many of the associations in this hybrid. The "off-spindle associations" demand further study concerning their mode of origin and significance, for it seems possible that they may result from nonhomologous pairing of threads at pachytene which has not resulted in chiasma formation (Elvers, 1934).

However, true bivalents do occur in this hybrid, with the bivalent partners held together by chiasmata at diakinesis and IM. Thus, the two pairs seen at diplotene in figure 12, *e*, and the one bivalent at diakinesis in figure 12, *f*, are typical bivalents with one chiasma and might be considered equivalent to certain bivalents in the parental species were it not for the difference in length of the conjugating chromosomes. That such bivalents cannot be a source of the majority of fragments seen at diakinesis and IM through crossing over in inverted segments or in segments having nonaligned insertion regions in the two chromosomes (Müntzing, 1935) is evident because the fragments are already formed and separated before the disjunction of the bivalents.

The irregularity in behavior of the chromosomes seen at diakinesis and IM is reflected in the first telophase and second metaphase. Thus, figure 12, *h*, shows a IT in which an equal number of chromosomes have been distributed to each pole, and five, two of which are drawn out, have lagged. Of the seven at the lower pole, one has already divided into daughter halves. Evidence that division of the individual chromosomes does not occur simultaneously but usually begins for some chromosomes at diakinesis and for others not until IIM, is shown by the PMC in figure 12, *i*, where nineteen chromosomes in each daughter nucleus are in various degrees of division and separation. Whether all the chromosomes will again undergo a longitudinal division in the ensuing metaphase is doubtful, but many of them appear ready for such a second division. This lack of uniformity in behavior in both the first and second divisions results in the formation of irregular numbers of pollen grains at cytokinesis. The sporad count showed only 13 per cent with four cells, all others having a greater number. Many of the tetrads had cells of unequal size. As would be expected from such behavior, this hybrid was completely sterile.

HYBRID BETWEEN THE 10-PAIRED SPECIES

The meiotic divisions of F_1 *N. longiflora* × *N. plumbaginifolia* were found to be regular, without multivalent formation, resulting in complete fertility of the hybrid. Evidence that the parental genoms differ in organization was obtained from diakinesis figures, where five bivalents were slightly heteromorphic (fig. 13).

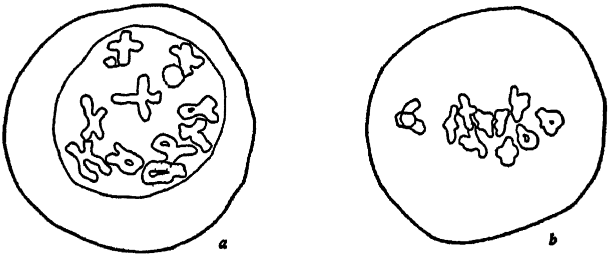

Fig. 13. PMC of F_1 *N. longiflora* × *N. plumbaginifolia*. *a*, diakinesis, 10_{II}, of which five are heteromorphic; *b*, IM, 10_{II}. × 1133.

DISCUSSION

The various types of evidence presented above concerning external morphology, distribution, genetic relations, chromosome number and morphology, and meiotic chromosome behavior in F_1 hybrids all indicate that the five 9- and 10-paired species of *Nicotiana* under discussion form a distinct assemblage within the genus. Hybrids between these species, with one exception, are rather easily obtained; hybrids between them and species not of this group, rarely. Two hybrids within this ALATA-GROUP are fertile and others are partly fertile, whereas all hybrids which have been made with species outside this group are sterile. The chromosome numbers of the ALATA-GROUP are unique in the genus, and suggest a closer relationship of these 9- and 10-paired species to one another than to any other chromosome number group in *Nicotiana.* Finally, with one exception, a high degree of chromosome conjugation occurs in F_1 intragroup hybrids, to show that in spite of differences in chromosome organization all the species of this group must possess a large number of "pairing blocks" of similar genes. The combined evidence therefore indicates that the ALATA-GROUP represents a phylogenetic unit, and at the same time it directs attention to the processes which have led to the establishment of distinctions between the species which compose it.

Of three important methods known to produce speciation, two, gene mutation and chromosome reorganization, have operated in the differentiation of the species of the ALATA-GROUP, the third method, polyploidy, not having been involved. That chromosome reorganization has been an important method of speciation is apparent from the differences between the species in chromosome morphology and number, and from the occurrence of multivalents in their hybrids. With respect to the three 9-paired species, the presence of a basic karyotype, the high amount of chromosome conjugation, and the fertility in their hybrids mean that the number of chromosome reorganizations which have occurred in the differentiation of these species from a common source are definitely limited. Thus *N. alata* and *N. Langsdorffii*, with the most marked differences in external and chromosome morphology, have the most regular chromosome conjugation and the greatest fertility in their hybrid, indicating that the distinctions between these two species in genic constitution and organization are not extensive. This is also shown by the Mendelian behavior of many character differences between the two species (Sachs-Skalinska, 1921). Nevertheless, we have definite evidence in the genoms of these species that at least three differences in chromosome organization, involving chromosome segments large enough to be visible, are present. The extent of multivalent formation in their F_1 hybrid confirms but does not extend this evidence, for the two translocations which could account for the distinctions in chromosome morphology could also account for the formation of a quinquivalent (figs. 6; 7, *a*, *b*). This means that changes of sufficient degree to produce differentiation of these two species in external morphology as a result of differences in genic constitution, and in chromosome morphology as a result of chromosome reorganization, have not destroyed the homology of blocks of genes of sufficient length to insure chromosome conjugation and chiasma formation.

In contrast to the situation in F_1 *N. alata* × *N. Langsdorffii*, we find in F_1 *N. alata* × *N. bonariensis* and in F_1 *N. Langsdorffii* × *N. bonariensis* that the number of chromosomes entering into multivalent formation exceeds the number of chromosomes differing in morphology in the parental genoms. In other words, visible differences in chromosome morphology between species may represent only a part of their differences in organization. But even the number of reorganizations necessary to account for the multivalents formed may be a minimum of those which have occurred, for, if translocations have involved pieces of chromosomes shorter than a certain length, they would not only fail to be visible as distinctions in the genoms, but also would not result in the formation of multivalents. In this connection it is to be noted that the composition of the multivalents formed in the 9-paired hybrids indicates that the formation of units larger than bivalents depends not only on the length of the regions involved in the translocations, but also on the lengths of the arms of the chromosomes in which they are situated. It is not just chance that the large A chromosomes with median insertion region take part in the multivalent formation characteristic of all these hybrids. While it is quite probable that these large chromosomes undergo more frequent and extensive reorganizations than the shorter ones, it is also true that these chromosomes regularly form a chiasma in each arm. If the end of one arm of an A chromosome large enough to permit chiasma formation is reciprocally translocated with a piece of equal length of another chromosome, the new translocated A will be able to form a chiasma with both of the original chromosomes. If, however, a segment of equal length is reciprocally translocated between the ends of two chromosomes with subterminal insertion regions, such as the B, C, and D of the 9-paired species, the new chromosomes will still possess only one long arm and will therefore be able usually to form only a single chiasma. They will rarely be able to express their reorganization in multivalent formation.

An examination of figure 6 will show that the multivalents formed in the 9-paired hybrids are terminated by short arms of chromosomes. It is probable that higher multivalents would have occurred if the parental species had possessed more large chromosomes with median insertion regions such as the A chromosomes. The infrequent occurrence of the septavalent in F_1 *N. Langsdorffii* × *N. bonariensis* (figs. 6 and 9, *a*) is likewise to be explained by the infrequent formation of chiasmata in short arms of chromosomes, since its formation in addition to two trivalents requires the production of two chiasmata in seven different chromosomes, whereas the average chiasma frequency per chromosome in the parental species is 1.6 and 1.2, respectively (table 2). The multivalents which occur in the 9-paired hybrids are thus indicators of translocations of a considerable size which have resulted in chromosomes with two arms each of sufficient length to form and maintain a chiasma. Accordingly, we can estimate approximately the number of larger reorganizations which have entered into the differentiation of the 9-paired species by determining the number of chromosomes which differ in morphology in the various complements, and the number of chromosomes which enter into multivalent formation in the hybrids. If smaller differences in organization exist between these species they cannot be detected by the methods used. It would be convenient if it could be shown that a certain number of distinctions in chromosome morphology are usually accompanied by a certain number of larger reorganizations which are not visible but may be expressed in multivalent formation and that this combined amount of detectable reorganizations is usually accompanied by a certain number of smaller, undetectable reorganizations. Actually, however, the evidences of speciation within the 9-paired group indicate that we cannot assume any uniform ratio of nonvisible to visible reorganizations, or of gene differences to chromosome reorganizations. The processes giving rise to these distinctions between species are going on concurrently, independently, and at different rates, in the various races, varieties, and species involved. The accumulated product at any one point in time is an individual matter, and all evidences of stability and change must be taken into consideration in order to obtain even a rough approximation of the degree of differentiation of the species concerned.

The accumulation of differences in genic constitution has played an important rôle in the differentiation of species of the ALATA-GROUP, as is indicated by the number of minor character differences even between *N. longiflora* and *N. plumbaginifolia,* species which clearly are closely related morphologically. By contrast, all other species of the group show many distinct character differences from one another. Nevertheless, the conspicuousness of such morphological distinctions must be due more to the prominence of characters affected than to the multiplicity of genic differences. In this connection Brieger (1930) has shown that in *N. alata, N. Forgetiana, N. Langsdorffii,* and *N. longiflora* striking differences in flower and pollen color have a very simple genic basis, which suggests that they have been differentiated from characters of an ancestral stock or from one another by relatively few factor mutations. Set apart most distinctly in features of external morphology is *N. Langsdorffii.* Indeed, in former taxonomic treatments of the genus this species was placed in the "Rustica section," in which other members of the ALATA-GROUP were not included (cf. Comes, 1899). That the pronounced distinctions between *N. alata* and *N. Langsdorffii,* for example, are not the result of a gradual accumulation of many gene differences each with a slight effect on the characters of external morphology is shown by the comparative regularity of chromosome conjugation and the fertility in their F_1 hybrids. It is possible, however, that relatively few gene differences affecting prominent external features could account for the morphological as well as the genetic characteristics of these species. Although the evidence available is not adequate to answer the question of the method of origin and accumulation of these few major genic differences, it does suggest that *N. Langsdorffii* might have had its origin in a cross of a 9-paired ancestral stock with an *N. rustica* ($n = 24$) race. The possibility of obtaining races with the chromosome number of one parent but with certain morphological features of the other has been demonstrated by Webber (1930). From a sesquidiploid hybrid of *N. Tabacum* (24) × *N. sylvestris* (12) with $2n = 60$, he obtained 24-paired races which resembled *N. Tabacum* but possessed certain characters derived from *N. sylvestris.* Apparently such races resulted from the substitution of certain *N. sylvestris* chromosomes for their homologues in the *N. Tabacum* complement with which they may conjugate in the sesquidiploid hybrid. Although *N. rustica* chromosomes presumably would show only occasional nonhomologous conjugation with the chromosomes of 9-paired species, a diploid gamete of a 9-paired stock uniting with a haploid gamete of *N. rustica* might give rise to a 9-paired race with a few new morphological characters introduced from *N. rustica* through a single or a few translocations between the two complements in the hybrid or its derivatives. Anastasia (1914) has suggested the "Petuniodes-Rustica" origin of *N. Langsdorffii,* and some such method as that just outlined would account both for the similarities between *N. rustica* and *N. Langsdorffii* and the differences between *N. Langsdorffii* and the other 9-paired species, without necessarily altering the extent or kinds of chromosome reorganization found to exist between these species (fig. 6). Whether or not hybridization outside the group has played a rôle in the origin of *N. Langsdorffii,* it differs at the present time from *N. alata* in relatively few genes which affect prominent morphological characters. *N. bonariensis,* on the other hand, may differ from *N. alata* in a greater number of genes than does *N. Langsdorffii,* but these have less pronounced effect upon prominent morphological characters.

The origin of the three 9-paired species from a common ancestral stock thus seems to be clearly indicated and must have involved both gene mutation and chromosome reorganization, but neither process has proceeded so far as to destroy their fundamental genic similarity. This is particularly clear with respect to their genoms, for the karyotype which they possess in common is distinct from that of all other species in the genus and is a clear indication of the common origin of these species (cf. fig. 1). What, then, can be said for the inclusion in this genetic group of *N. longiflora* and *N. plumbaginifolia,* whose genoms are distinct from those of the 9-paired species in both chromosome number and morphology? We have seen that their distribution overlaps that of the 9-paired species In features of external morphology, Millan (1928) has noted that *N. alata* is close to *N. longiflora.* Brieger (1930) has concluded that *N. longiflora* contains genes which are allelomorphic and similar in their effect to those in the 9-paired species. Malloch and Malloch (1924) found that most characters of *N. longiflora* behaved as recessives to those of *N. Sanderae* in the hybrid between these species. Finally, the regularity in chromosome conjugation in hybrids of *N longiflora* with *N. alata* and *N. Langsdorffii* is perhaps the most definite evidence we have of the basic homology of the genoms of these species. This fourfold indication of a common origin of the 9- and 10-paired species leaves unanswered only the question of the source of their present distinctions in chromosome number and morphology.

Lewitsky (1931*b*) has pointed out that great differences in genom between closely related species must have been rapidly established through chromosome reorganizations. The reorganizations necessary to produce the differences in genom between the 9- and the 10-paired species of the ALATA-GROUP are extensive, yet they must have occurred over a period of time not great enough to allow the accumulation of genic differences usually accompanying such extensive changes. According to Delauney's (1926) classification, the origin of the *N. longiflora* genom must have involved sudden "revolution" expressed in a complete transformation of the whole nucleus and would, therefore, suggest that *N. longiflora* and *N plumbaginifolia* should constitute a separate genus. However, the demonstrated evidence of their fundamental relationship to the 9-paired species would not justify such procedure and leads to the conclusion that the present gap between the karyotypes of the 9- and 10-paired species is due to the disappearance of intermediate members.

Although the chromosome reorganizations which are reflected in the distinctions between the 9- and 10-paired species must be great, affecting nearly every chromosome in the genom, they need not be different from those which have been described as concerned in the less profound differentiation of the genoms of the 9-paired species. Any advantage in the possession of a complement with chromosomes all of one type, as in *N. longiflora,* would assure the rapid establishment and preservation of this genom (cf. Upcott and La Cour, 1936). It is conceivable that in its effect upon number, position, and terminalization of chiasmata, and upon uniformity in rate of disjunction of bivalents and daughter chromosomes, which would influence the regularity and rate of meiosis and mitosis, the possession of chromosomes all with subterminal insertion regions might aid in the rapid establishment and preservation of species with karyotypes such as those of *N. longiflora* and *N. plumbaginifolia.*

The transformation of a 9-paired genom in which more than half the chromosomes have median or submedian insertion regions into a 10-paired genom in which all the chromosomes have subterminal insertion regions would then be hastened by the selection of reorganizations resulting in the establishment of such insertion regions without necessarily involving loss or change in the genic constitution of the race. Such a derivation of a 10-paired from a hypothetical 9-paired ancestral stock, rather than the reverse process, is in accord (1) with Lewitsky's conclusion that biarmed chromosomes are primitive whereas "headed" chromosomes are derived, (2) with Malloch and Malloch's observation that *N. longiflora* characters are predominately recessive to those of a 9-paired species (*N. Sanderae*), and (3) with the evidence that *N. longiflora* is rapidly extending its range of distribution and is, therefore, of recent origin.

The 9- and 10-paired species of *Nicotiana* thus form a genetic group in which the species are more closely related to one another than they are to any other species of the genus. The present evidences of this relationship can best be accounted for by their derivation from a common ancestral 9-paired stock through the accumulation of differences in genic constitution and organization. The number and kinds of distinctions, morphological, genetic, and cytological, between any two species are not the same as those between any other two species within the group. Two species each of which differs from a third species to approximately the same degree in features of their external morphology do not show the same number of differences in the morphologies of their chromosomes, or the same amount of chromosome conjugation, or sterility in their F_1 hybrids. The fact that these four evidences of relationship are not the same for any two pairs of species means that in the differentiation of these species there has not been uniformity in the length of time involved, in the rate of establishment of changes, or in the rôles played by gene mutation and chromosome reorganization.

SUMMARY

1. *Nicotiana alata, N. bonariensis, N. Langsdorffii, N. longiflora,* and *N. plumbaginifolia* possess certain morphological characters in common, have a distinct center of distribution, produce intragroup F_1 hybrids some of which are fertile or partially fertile, and are distinguishable from other *Nicotiana* species in respect to chromosome number and morphology. Therefore these species are considered to constitute a phylogenetic unit within the genus, the ALATA-GROUP. Low chromosome numbers, distinctions in chromosome number and morphology, and multivalent formation in the F_1 hybrids make possible the study of speciation mechanisms operative in *Nicotiana.*

2. The nature of the karyotype serves to subdivide the species of the ALATA-GROUP, *N. longiflora* and *N. plumbaginifolia* forming a 10-paired section and *N. alata, N. bonariensis,* and *N. Langsdorffii* a 9-paired section. In the 10-paired species all the chromosomes are of one morphological type. In the 9-paired species the basic karyotype consists of four morphologically distinct

types of chromosome, the genoms of the three species showing visible differences from one another.

3. Bivalent configurations and chiasma frequencies in four of the species were found to be determined by the position of the insertion region and the length of the arms of the chromosomes concerned.

4. A high degree of chromosome conjugation occurs in six of the seven intragroup F_1 hybrids investigated, multivalents as well as bivalents usually being formed. The occurrence of these multivalents, consisting of three to seven chromosomes, indicates that although the species differ in genic organization their basic genic constitution is similar.

5. In the hybrids between 9-paired species the formation of units larger than bivalents depends not only on the size of regions involved in reorganizations, but also on the lengths of the arms of the chromosomes in which they are located. In hybrids between 9- and 10-paired species the occurrence of heteromorphic bivalents and trivalents indicates homology between shorter chromosomes with subterminal insertion region in the 10-paired species and one arm of large chromosomes with median insertion region in the 9-paired species.

6. Evidence suggesting that the 10-paired species may have been derived from a 9-paired ancestral stock, and the rôles which gene mutation and chromosome reorganization appear to have played in the differentiation of the species of the ALATA-GROUP, are discussed.

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A FOURTH NEW SPECIES OF NICOTIANA FROM PERU

BY

T. H. GOODSPEED

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T. H. GOODSPEED

THE FIRST University of California Botanical Garden Expedition to the Andes (1935–1936) found a number of new species and varieties of *Nicotiana* in Peru (cf. Goodspeed, 1938), and members of the second expedition (1938–1939), who collected there extensively, discovered still other previously unknown material. The new species of *Nicotiana* described in the present paper was not, however, collected by either expedition, but by Mr. Bayne Beauchamp of Berkeley, California, on his return journey after an exploration of parts of the Oriente of northeastern Peru.

In his letter of August 19, 1937, from Pto. Chicauma, Peru, Mr. Beauchamp refers to collecting this new species "along the trail between Chachapoyas and Leinebamba[1] during my second day's journey from Chachapoyas. All appeared to be of the same variety—unusually tall and branching—one specimen was twice my height on horseback and many others were well over six feet. The leaves were moderately small for tobacco, the florescence hearty. ... There were no fields of tobacco in this region. The plants were growing and dying without notice. I saw no evidence that they were or ever had been cultivated or domesticated. Further back toward the Huallaga, east of Moyobamba, I saw fields of domesticated tobacco, but it was a broad-leafed variety, very different."

From lack of time Mr. Beauchamp was unable to collect herbarium specimens of this *Nicotiana,* nor is it represented in the major herbaria in North or South America or in Europe. The description of this interesting and showy species is, therefore, based entirely on cultures grown in the University of California Botanical Garden from seed collected by Mr. Beauchamp

Two cultures from the original seed have been grown, C-057 and D-131. Of a total of sixty plants set out, thirty-nine proved to be the new species and twenty-one a dark pink-flowered race of *N. Tabacum.* In conversation Mr. Beauchamp has recently told the author that a few hours after collecting the seed of what has proved to be a new species of *Nicotiana* he saw growing near native huts a few plants which at the time he thought resembled those along the trail from which he had just before taken seed. He therefore picked a ripe capsule or two from these plants, which undoubtedly were *N. Tabacum* escaped from cultivation, and placed them in his pocket with the seed previously collected. This information explains the occurrence of both species in our cultures from seed collected by Mr. Beauchamp.

Nicotiana Setchellii sp. nov.

Planta subarborescens perennis viscida; folia oblongo-oblanceolata lanceolato-ellipticave sessilia vel brevipetiolata petiolis alatis, basi subauriculata paullo decurrentia; inflorescentia paniculiformis pedicellis in fructu conspicue curvatis; flores magni corollarum apicibus in alabastris manifestis; corolla infundibularis paullo flexa, limbo faucibusque conjunctis campanulatis; stylum et stamina inclusa ad partem inferioram corollae accedentia.

---

[1] Undoubtedly should read "Leimebamba."

Type.—University of California Herbarium Nos. 639057–060. University of California Botanical Garden C-057P$_3$, July 12, 1940, cultivated from seed collected by Bayne Beauchamp, August, 1937, along the trail between Chachapoyas and Leimebamba on his second day's journey from Chachapoyas, Depto. Amazonas, Peru.

Massive, subarborescent or shrubby, soft-woody perennial 2–5 m. high. Stem erect, 4–6 cm. in diameter, light yellow-green, viscid-pubescent with numerous short, soft, simple and branched glandular hairs, in age thinly corky, greenish gray to grayish brown, striated by many shallow furrows and marked by leaf scars; first branches chiefly subterminal, oblique, forming narrow crown, later branches scattered, numerous, long, oblique or ascendent. Leaves coarse but not fleshy, close-ranked (internodes 2–6 cm. long), mostly horizontal or curving downward, 4–7 dm. long, 2–3 dm. wide, oblong-oblanceolate or lanceolate-elliptic, sessile or with short, winged petiole, base somewhat auricled, shortly decurrent, apex acute or acuminate, margin undulate, both surfaces covered with rather dense, inconspicuous indument of short hairs (both branched and simple), upper surface glossy, rugulose, rather dark green, not viscid, lower dull, lighter green, more or less viscid. Inflorescence usually rather compact, 5–7 dm. long, 4 dm. broad, paniculiform, single stout, viscid central axis 5–10 mm. in diameter, laterals slender, numerous (30 ±), oblique, lower ones occasionally forked, 20–30 cm. long, about 10 cm. apart, then progressively shorter, closer, seldom or never forked; pedicels secund, approximate, 10–15 mm. long, viscid-pubescent, directing flowers obliquely upward and outward, later curving upward and inward in erect inflorescences, directing capsules toward main axis of inflorescence, in horizontal inflorescences capsules more or less vertical, not convergent; lowest two or three bracts foliaceous, about 25 cm. long, 10 cm. wide, obcuneate, continuing without contraction into decurrent wings, upper bracts much smaller (20–80 mm. long, 7–15 mm. wide), narrower, less decurrent, prolonged acuminate from much dilated base, ultimate bractlets 4–5 mm. long, 1–2 mm. wide, narrowly obcuneate, curved; flowers abundant, peripheral, odorless. Calyx dull yellow-green, with or without reddish (amaranth purple[2]) flush, pubescent, sometimes viscid, cylindric with rounded base, 20–28 mm. long, 10 mm. wide, segments unequal, narrowly triangular-acuminate, 5–15 mm. long, erect or nearly so. Corolla broadly, asymmetrically infundibular, slightly flexed at juncture of tube with throat and limb, texture coarse, outer surface more or less viscid to varnished; tube 15–25 mm. long, 8 mm. wide, indented below stamen insertions, outer surface white to pale greenish yellow (chalcedony yellow) within calyx, usually more reddish and greenish above it, inner surface glossy white with pale pink or pale green flush; throat an oblique cup 15–18 mm. long, 12–15 mm. wide, gradually merging with limb on upper side of flower, sharply defined on lower, pale greenish yellow (chalcedony yellow) within, sometimes with flush of pink, outer surface reddish or pinkish (russet vinaceous to pomegranate purple or Eugenia red), sometimes slightly bronzed by amber-headed glandular hairs and usually more yellow-green on lower side of flower; limb spirally plicate in bud with evident lobe apices, later forming bowl 35–50 mm. across, 10–15 mm. deep, within uniformly pinkish or reddish (pink to Eugenia red or deep vinaceous) from abrupt erose boundary near mouth out to margin, margin sometimes darker, outer surface of limb generally darker and more bronzed, color merging gradually into that of throat, lobing shallow, segments broadly triangular (rarely broadly ovate), apices conspicuously acuminate. Stamens inserted unequally or subequally on corolla tube 5–8 mm. from its base, of three lengths, one not reaching apex of throat or only barely exceeding it, two to 1–3 mm. beyond, two to 3–5 mm. beyond, even longest pair included within corolla limb, filaments subsigmoid, oriented against lower side of flower, whitish, yellowish green, pale pink, or any combination of these, glabrous throughout or lowest 4–5 mm. clothed with short, distinct, soft hairs; anthers commonly massed against lower side of corolla limb, greenish yellow, large (8 mm. long, 4 mm. wide), suboblong, flattened, versatile, filament attachment well below middle. Pollen ivory to pale straw color. Hypogynous disk thick, pale or light yellow; ovary ovoid-elliptic, 7 mm. long, 6 mm. wide, pale greenish yellow (pale viridine yellow) with or without pink flush or marking, to reddish or reddish purple (amaranth purple or pansy purple); style pale yellowish green, lower part curved slightly, placing upper part against lower side of flower, otherwise straight; stigma sometimes not reaching distal end of most exserted pair of anthers, sometimes several mm. beyond them, acute, compressed, shallowly lipped, receptive surface bright green. Capsule included, elliptic, 15–20 mm. long, 8–10 mm. wide, walls light greenish, on drying brownish, thin but firm, two valves sometimes remaining attached to each other at apex, sometimes not, in either case separating from there to point even with top of calyx. Both style and corolla characteristically persistent on mature, dehisced capsule. Seeds numerous, subrotund, broadly elliptic or elliptical-oval, about 0.5–0.6 mm. long, dull brown, surface shallowly reticulate with moderately large, lobed meshes, embryo straight. Chromosome number twelve pairs.

---

[2] Colors referred to in parentheses are in accordance with Ridgway (1912).

A genetic group in *Nicotiana* called the "tomentosa group" (cf. Goodspeed, 1940) includes, among other species, *N. tomentosa* R. & P., *N. tomentosiformis* Goodsp., and *N. otophora* Griseb., all of which are more or less closely related, as indicated by both morphological and cytogenetic evidence. With these species *N. Setchellii* has many affinities. From any conspecific relationship with any one of them it may, however, be readily distinguished by the larger, coarser, more campanulate corolla, the less exserted and differently oriented stamens, and the nature of its inflorescence. In flower form its resemblance to *N. Tabacum,* while not marked, is considerable.

The description of *N. Setchellii* given above includes definition of the range of variation in leaf and flower characters (cf. plate 15) exhibited by the plants grown from the original seed. Elsewhere the extreme polymorphism of *N. tomentosa* and other members of the "tomentosa group" is being described. It may here be noted that, although not so polymorphic as *N. tomentosa,* which has been grown in more than twenty-five different cultures from seed collected at various points over its extensive distributional range in Peru, *N. Setchellii* is more variable in certain morphological characters than any member of the other genetic groups in *Nicotiana* grown from a single seed collection involving one or more than one plant. Establishment of races pure breeding for at least certain extremes of the morphological variation described is, however, rapid. Thus, in the second generation from a plant of one of the cultures from original seed which was characterized by the rather distinctive leaf shape shown at the extreme right in plate 15, figure 2, a population of twenty-five plants all showed this parental leaf type.

The tomentosa group is notably late in reaching maturity. *N. tomentosa,* the most extreme of the group in this regard, generally flowers in the second year, *N. tomentosiformis* begins blooming in the first winter, and *N. otophora* is variable, but, if sown sufficiently early, will flower the first fall. *N. Setchellii* regularly is in bloom in the fall of the same year in which it is sown. Once begun, its blooming continues practically without interruption, and the transition from the simpler juvenile habit (pl. 14, fig. 1) to a large, symmetrical, treelike shrub with showy inflorescences terminating each of its many branches (pl. 14, fig. 2) is rapid.

The maximum life span of individual plants of *N. Setchellii* is not known. The thick stems are easily snapped by strong wind even after attaining considerable age and woodiness (cf. pl. 14, fig. 2). However, the persistence of *N. Setchellii* in a favorable environment would be especially favored both by its heavy set of selfed seed and by its ability to rootsprout prolifically. In the second year of its growth in the Botanical Garden in Berkeley, a single plant of *N. Setchellii* will be surrounded for distances up to forty feet by from twenty to thirty young plants the origin of which from roots can be readily traced. Under favorable conditions in the Peruvian Andes, a related species, *N. tomentosa,* rootsprouts vigorously and the heavy stands of this species seen there are almost entirely the result of this mode of vegetative propagation. Grown in Berkeley, *N. tomentosa* behaves in the same fashion.

The occurrence of this new species in Depto. Amazonas is of particular interest in that it extends northward in Peru some two hundred miles, without connection, the geographical range of the semiarborescent members of the tomentosa group. How extensive the area occupied by *N. Setchellii* will prove to be and whether or not it ultimately will be found to touch at any point or extend over the northern boundary of *N. tomentosa,* remains to be determined.

Nicotiana Setchellii is named in honor of Dr. W. A. Setchell, Professor of Botany, Emeritus, University of California, who has continuously encouraged the investigations of the genus *Nicotiana* which he began some forty years ago. I am greatly indebted to Mr. Beauchamp for bearing in mind my desire to obtain *Nicotiana* material from Peru and for turning over to me the seed collection which has brought to light the existence of *N. Setchellii.*

The investigation reported upon above was aided by a grant from the Committee on Research, University of California, and by the personnel of Work Projects Administration Official Project No. 65-1-08-91, Unit B-3.

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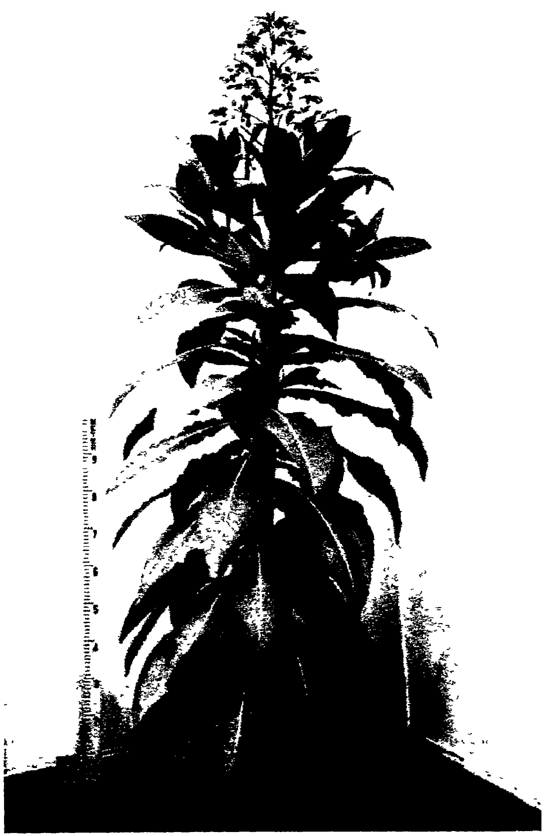
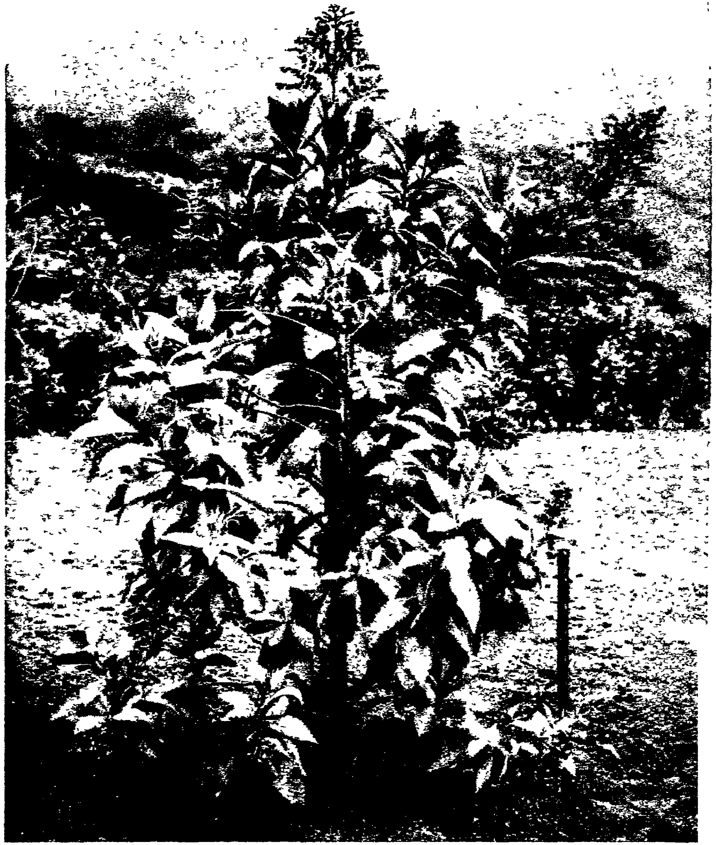
PLATES

PLATE 14

Fig. 1. A young plant of *Nicotiana Setchellii* coming into the height of its first flowering; the development of lateral branches proceeding downward.

Fig. 2. A plant of *N. Setchellii* in its second year. The original main axis has been broken below the present uppermost inflorescence and the condition of lateral branches somewhat altered by winter winds.



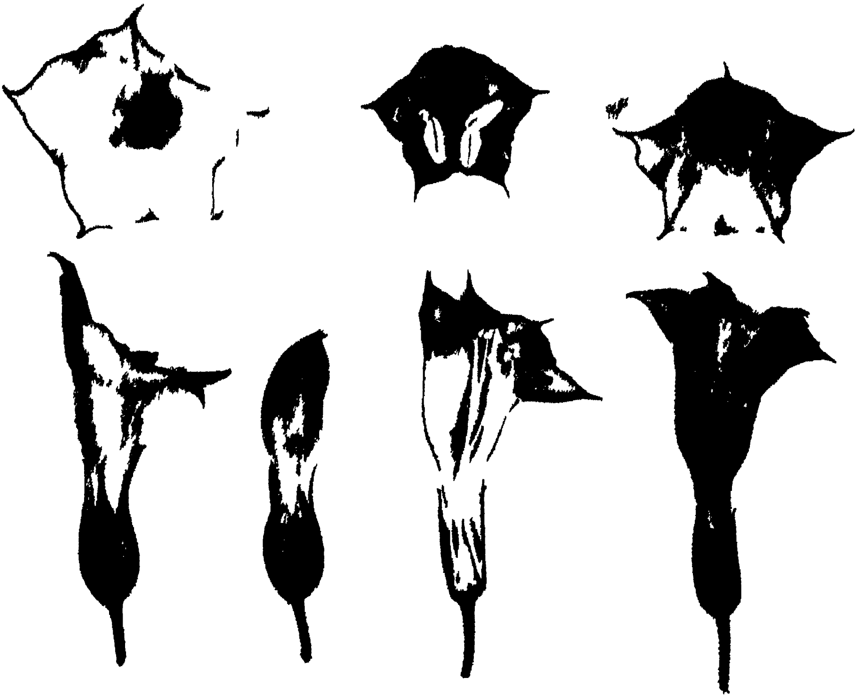


2

PLATE 15

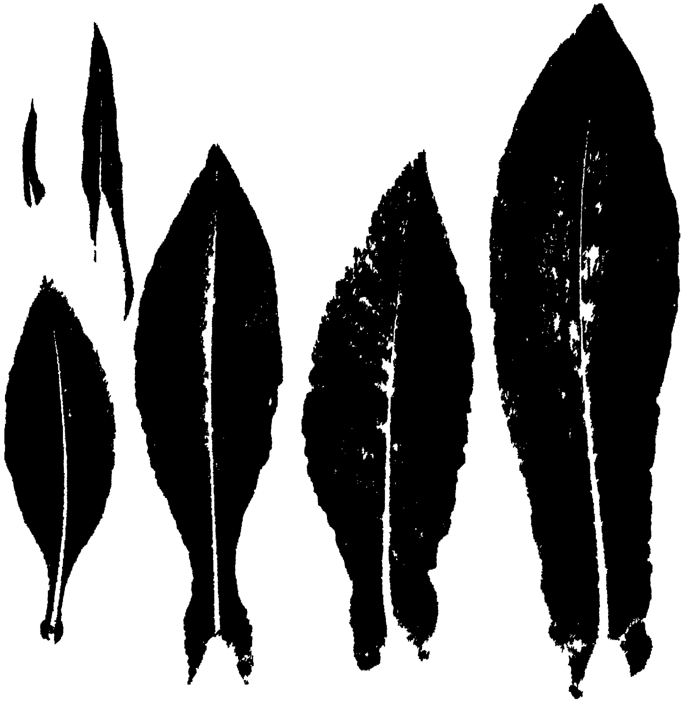
Fig. 1. Flower structure and variation. Left: mature flower and bud from C-057P_7. Right: incompletely and completely expanded flowers from C-057P_9, the former split to show pistil, stamens, and color pattern. Note range of variation in color and calyx characters.

Fig. 2. Leaf shape. Above, two bracts from the same inflorescence. Below, four leaves from four different plants. At the extreme left, venation on the under surface is shown.



1

C-057



CHROMOSOME NUMBERS IN THE HYDROPHYLLACEAE

BY

MARION S. CAVE AND LINCOLN CONSTANCE

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BY

MARION S. CAVE AND LINCOLN CONSTANCE

A SURVEY of chromosome numbers occurring in the Hydrophyllaceae has been undertaken in conjunction with systematic studies of the family being conducted by Constance. It is hoped that any facts gained in this way may prove to be of assistance in delimiting taxonomic units and in determining natural relationships within the family. All the preparations, counts, and camera lucida drawings have been made by Cave; Constance has been responsible for securing most of the material investigated, and for all identifications.

Several chromosome counts referable to members of the family occur in Tischler's lists (1929, 1931, 1938), or have been reported in other papers. Most counts, however, have been based upon garden material or commercial seed of uncertain source, and no specimens are available for checking the identity of the plants involved. Such counts can be of little value taxonomically unless bolstered by carefully preserved herbarium specimens. When previously reported counts disagree with our own, we can only suggest the possibility that earlier authors may have mistaken the identity of their plants. All the published numbers of which we have been able to learn are tabulated in table 1. Some of the names in the original publications have been corrected.

All of the new counts reported here have been obtained from pollen mother cells, fixed in Carnoy's acetic alcohol, dissected from young anthers in the flower buds, and smeared in acetocarmine. The buds were collected in the field, together with numbered sets of specimens, and every chromosome count is firmly attached to its herbarium specimen deposited in the University of California Herbarium. It is intended to accentuate that connection by affixing each chromosome figure drawn, some of which are used in this paper, directly to the herbarium specimen with which it was collected. In this way cytologists may be encouraged to greater appreciation of the value of herbaria, and taxonomists may be made more aware of the systematic value of cytological evidence. The numerous duplicates of these collections either have been or ultimately will be distributed to leading herbaria.

The recent revisions by Constance of the genera *Eucrypta* (1938), *Hydrophyllum* (1942), *Nemophila* (1941), and *Pholistoma* (1939) are the bases for determinations of plants in these groups. The identifications in *Phacelia* are extremely tentative, since chromosome counts and other evidence indicate that extensive modification of accepted sectional and specific lines may be necessary before satisfactory naming will be possible. At present, it is only possible to refer the plants whose chromosomes were counted to the described segregates most similar to them morphologically. For convenience the species are arranged in accordance with the sectional divisions adopted by Brand (1913).

Certain of the names employed are untenable, but we here wish to avoid suggesting new names and combinations.

The results of our own investigations, to date, are presented in table 2 and in the text figures. Only a very small proportion of the members of the family have been investigated cytologically. We hope to be able to continue our survey and to extend it to every genus and as many species as possible.

TABLE 1

PREVIOUSLY REPORTED CHROMOSOME NUMBERS IN THE HYDROPHYLLACEAE

Species	Number		Authority
	n	2n	
Hydrolea spinosa L.	20		Svensson 1925.
Hydrophyllum canadense L.	9		Winkler (ex Tischler 1921–22).
Hydrophyllum virginianum L.		18	Bowden 1940[1].
Nemophila maculata Benth.	9		Chittenden and Turrill 1926; Chittenden 1928; Sugiura 1928[1].
Nemophila Menziesii H. and A.	9		Chittenden and Turrill 1926; Chittenden 1928; Sugiura 1928[1], 1936*a*, 1936*b*[1].
var. *atomaria* (F. and M.) Chandl.	9		Chittenden and Turrill 1926; Chittenden 1928; Sugiura 1928[1].
Phacelia campanularia Gray	11		Sugiura 1936*b*[1]; Chittenden 1928[2].
Phacelia ciliata Benth.	9		Sugiura 1940.
Phacelia circinata Jacq.	11		Sugiura 1940.
Phacelia congesta Hook.	9		Sugiura 1928[1].
Phacelia divaricata (Benth.) Gray	10		Sugiura 1940.
Phacelia minor (Harv.) Macbr.	11		Chittenden 1928[2]; Sugiura 1940.
Phacelia Parryi Torr.	11		Chittenden 1928[2].
Phacelia tanacetifolia Benth.	9		Tjebbe 1928.
	11		Sugiura 1936*b*[1].
Phacelia viscida (Benth.) Torr.	11		Chittenden 1928[2].
Pholistoma auritum (Lindl.) Lilja	12		Svensson 1925.
	9		Chittenden 1928.
Wigandia Vigieri Carr.	22		Sugiura 1936*a*, 1936*b*[1].

[1] Figured.
[2] By implication only.

The data already obtained indicate that *Hydrophyllum, Nemophila,* and *Pholistoma* all have a chromosome complement of nine pairs. A large, tardily dividing chromosome was observed in all of the material of *Pholistoma* examined. The chromosomes of *Hydrophyllum* are larger than those of the other nine-paired genera. The chromosomal pattern in *Phacelia,* the largest and most varied genus of the family, is far more complex. Counts of eight, nine, ten, eleven, thirteen and twenty-two pairs have already been revealed, and still others may occur. Chromosome size also varies greatly in this genus. A large number of counts made on sample members of the *Phacelia magellanica-californica-heterophylla* complex indicate that the confusing morphological diversity and intergradation within this "taxonomically difficult" group is due, at least in part, to the occurrence of polyploidy.

TABLE 2

CHROMOSOME NUMBERS IN THE HYDROPHYLLACEAE

(From the present study)

Name	n number	Locality	Collector
Hydrophyllum			
appendiculatum Michx.	9	Clay Co., Ky.	*Baldwin, Harvill and Shacklette*
capitatum Dougl. var. *alpinum* Wats.	9	Hobart Mills, Nevada Co., Calif.	*Stebbins* 2998
Fendleri (Gray) Heller	9	Lawyer Creek Canyon, Lewis Co., Idaho	*Constance and Beetle* 2740
occidentale (Wats.) Gray	9	Low Gap, Trinity Co., Calif.	*Constance and Beetle* 2616
tenuipes Heller (purple-flowered)	9	Big Creek, Clatsop Co., Ore.	*Constance and Beetle* 2662
(greenish flowered)	9	Van Duzen River, Humboldt Co., Calif.	*Constance and Beetle* 2611
Pholistoma			
auritum (Lindl.) Lilja	9	Abbots, Monterey Co., Calif.	*Constance and Hoover* 2060
membranaceum (Benth.) Const.	9	Jamesburg, Monterey Co., Calif.	*Constance and Hoover* 2054
	9	Kern Canyon, Kern Co., Calif.	*Mathias* 1321, 1322
Nemophila			
breviflora Gray	9	Thombs Creek, Modoc Co., Calif.	*Constance* 2332
heterophylla F. and M.	9	Berkeley Hills, Alameda Co., Calif.	*Constance and Mason* 2031
	9	Howell Mts., Napa Co., Calif.	*Constance* 2035
	9	Putah Creek, Yolo Co., Calif.	*Constance* 2045
Menziesii H. and A.	9	Claremont Creek, Alameda Co., Calif.	*Constance and Mason* 2032
parviflora Dougl.	9	Navarro River, Mendocino Co., Calif.	*Constance* 2509
var. *Austinae* (Eastw.) Brand	9	Thombs Creek, Modoc Co., Calif.	*Constance* 2333
var. *quercifolia* (Eastw.) Chandl.	9	Chilkoot Creek, Madera Co., Calif.	*Constance* 2366
pedunculata Dougl.	9	Clear Creek, Douglas Co., Nev.	*Mathias* 1374
	9	Jamesburg, Monterey Co., Calif.	*Constance and Hoover* 2051
pulchella Eastw.	9	North fork Tule River, Tulare Co., Calif.	*Constance and Mason* 2123
	9	Pinehurst, Fresno Co., Calif.	*Constance* 2219
var. *fremonti* (Eastw.) Const.	9	Hobo Hot Springs, Kern Co., Calif.	*Constance and Mason* 2117
Eucrypta			
micrantha (Torr.) Heller	9	Salt Wells Canyon, San Bernardino Co., Calif.	*Constance and Mason* 2115

TABLE 2—(*Continued*)

Name	n number	Locality	Collector
Phacelia			
Section Whitlavia			
minor (Harv.) Macbr.	11	Santa Ana River, San Bernardino Co., Calif.	*Constance* 2803
	11	Lone Pine Canyon, San Bernardino Co., Calif.	*Constance and Peirson* 2852
Section Euphacelia			
ammophila Greene	11	Point Reyes, Marin Co., Calif.	*Constance and Killip* 2838
Breweri Gray	11	Mount Diablo, Contra Costa Co., Calif.	*Constance and Morrison* 2191
ciliata Benth.	11	La Panza, San Luis Obispo Co., Calif.	*Constance and Beetle* 2535
distans Benth.	11	Grizzly Peak, Alameda Co., Calif.	*Constance* 2563
	11	Arroyo del Puerto, Stanislaus Co., Calif.	*Constance and Hoover* 2808
var. *australis* Brand	11	Santa Ana River, San Bernardino Co., Calif.	*Constance* 2802
eximia Eastw.	11	Wheeler Hot Springs, Ventura Co., Calif.	*Constance* 2843
hispida Gray var. *heliophila* Macbr.	11	Ortigalita Canyon, Merced Co., Calif.	*Constance and Morrison* 2575
humilis T. and G.	11	Cedarville Pass, Modoc Co., Calif.	*D. E. Beetle* 65
irritans Brand	8	Emigrant Gap, Placer Co., Calif.	*Stebbins and Babcock* 1583
loasaefolia Benth.	11	Gorda, Monterey Co., Calif.	*Constance* 2840
malvifolia C. and S.	11	Stinson Beach, Marin Co., Calif.	*Constance and Beetle* 2814
ramosissima Dougl.	11	Condon, Gilliam Co., Ore.	*Constance and Beetle* 2704
tanacetifolia Benth.	11	Mojave, Kern Co., Calif.	*Constance and Mason* 2109
	11	McLure Valley, Kings Co., Calif.	*Constance and Beetle* 2544
magellanica-californica-heterophylla complex			
argentea Nels. and Macbr.	22	Pistol River, Curry Co., Ore.	*Constance and Beetle* 2625
californica Cham.	22	Table Bluff, Humboldt Co., Calif.	*Constance and Beetle* 2609
	22	Point Richmond, Contra Costa Co., Calif.	*Constance* 2524
compacta Greene	22	Island Lake, Elko Co., Nev.	*Beach and Mills* 1393
heterophylla Pursh	11	Empire, Mendocino Co., Calif.	*Constance and Beetle* 2606
	22	Magalia, Butte Co., Calif.	*Constance* 2829
	11	Clear Creek Canyon, Ormsby Co., Nev.	*Stebbins* 3002
	11	Bridgeville, Humboldt Co., Calif.	*Stebbins* 3111
	11	Days Creek, Douglas Co., Ore.	*Gould and Beach* 1085
imbricata Greene	22	Sexton Mountain, Douglas Co., Ore.	*Gould and Beach* 1065
	11	Cuesta Grade, San Luis Obispo Co., Calif.	*Stebbins* 3071

TABLE 2—(*Concluded*)

Name	n number	Locality	Collector
Phacelia—(*Continued*)			
	22	Arroyo del Puerto, Stanislaus Co., Calif.	*Constance and Hoover* 2810
	11	Clinton, Amador Co., Calif.	*Constance* 2818
	11	Marysville Buttes, Sutter Co., Calif.	*Constance* 2833
	22	Big Sur, Monterey Co., Calif.	*Constance* 2839
	11	Wheeler Hot Springs, Ventura Co., Calif.	*Constance* 2845
	11	Lake Arrowhead road, San Bernardino Co., Calif.	*Constance and Peirson* 2846
	11	Baldwin Lake, San Bernardino Co., Calif.	*Constance and Peirson* 2849
	11	Greenhorn Range, Kern Co., Calif.	*Constance* 2857
leucophylla Torr.	22	Boardman, Morrow Co., Ore.	*Cave* 4104
	11	Cedarville Pass, Modoc Co., Calif.	*D. E. Beetle* 67
mutabilis Greene	22	Lake Almanor, Plumas Co., Calif.	*A. A. Beetle* 2778
nemoralis Greene	22	Sauvies Island, Multnomah Co., Ore.	*Constance and Beetle* 2674
Section Eutoca			
divaricata (Benth.) Gray	10	Berkeley Hills, Alameda Co., Calif.	*Constance and Nelson* 2571
mohavensis Gray	9	Baldwin Lake, San Bernardino Co., Calif.	*Constance and Peirson* 2848
	9	Vincent Gulch, San Bernardino Co., Calif.	*Constance and Peirson* 2855
procera Gray	11	Peshastin Creek, Chelan Co., Wash.	*Constance and Beetle* 2753
sericea (Graham) Gray	11	Many Glacier, Glacier Park, Mont.	*Cave* 4115
Section Microgentes			
Fremontii Torr.	13	Lancaster, Los Angeles Co., Calif.	*Constance* 2801
Emmenanthe			
penduliflora Benth.	18	Lone Pine Canyon, San Bernardino Co., Calif.	*Constance and Peirson* 2853
Romanzoffia			
Suksdorfii Greene	11	Cataract Gulch, Marin Co., Calif.	*Constance and Beetle* 2570

Figure A. Chromosomes of Hydrophyllum, Pholistoma, Nemophila, and Eucrypta. × 1150.

1. *H. appendiculatum,* Diak.; *Baldwin, Harvill and Shacklette.*
2. *H. capitatum* var. *alpinum,* Diak.; *Stebbins* 2998.
3. *H. Fendleri,* II M; *Constance and Beetle* 2740.
4. *H. occidentale,* Diak.; *Constance and Beetle* 2616.
5. *H. tenuipes,* Diak.; *Constance and Beetle* 2611.
6. *H. tenuipes,* Diak.; *Constance and Beetle* 2662.
7, 8, 9. *P. auritum,* I A, I T, I A; *Constance and Hoover* 2060.
10, 11. *P. membranaceum,* I M, I A; *Constance and Hoover* 2054.
12. *N. heterophylla,* II M; *Constance* 2035.
13. *N. breviflora,* II T; *Constance* 2332.
14. *N. pulchella,* II M; *Constance and Mason* 2123.
15. *N. pulchella* var. *fremonti,* II T; *Constance and Mason* 2117.
16. *N. Menziesii,* II M; *Constance and Mason* 2032.
17. *N. parviflora* var. *Austinae,* II M; *Constance* 2333.
18. *N. pedunculata,* I T; *Constance and Hoover* 2051.
19. *N. parviflora* var. *quercifolia,* II M; *Constance* 2366.
20. *N. parviflora,* II M; *Constance* 2509.
21. *Eucrypta micrantha,* I M; *Constance and Mason* 2115.

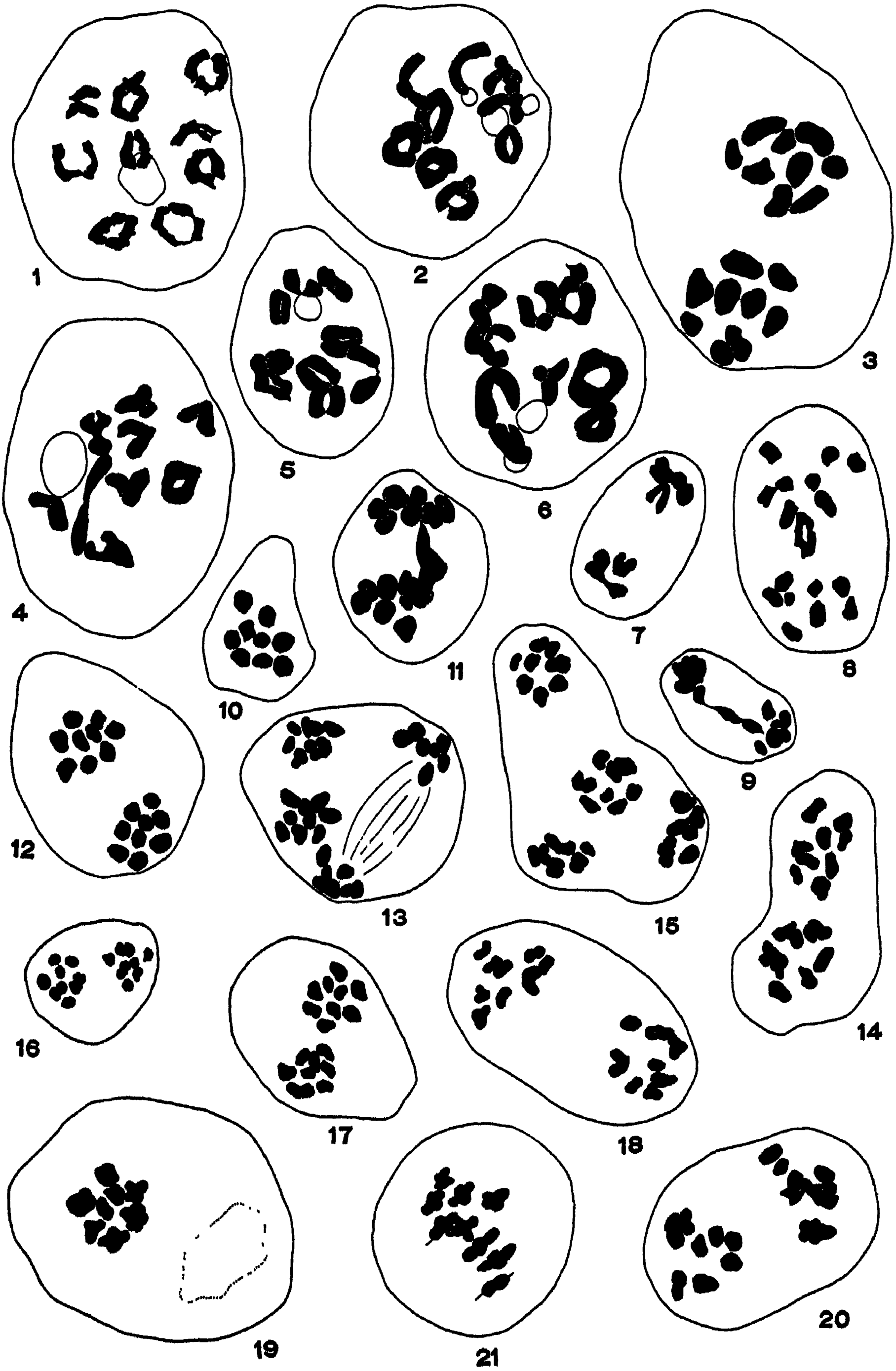

Figure A

Figure B. Chromosomes of representative Species of Phacelia, Emmenanthe, and Romanzoffia. × 1150.

22. *P. minor,* II M; *Constance and Peirson* 2852.
23. *P. divaricata,* Diak.; *Constance and Nelson* 2571.
24. *P. procera,* II M; *Constance and Beetle* 2753.
25. *P. irritans,* II M; *Stebbins and Babcock* 1583.
26. *P. sericea,* II M; *Cave* 4115.
27. *P. mohavensis,* I T; *Constance and Peirson* 2855.
28. *P. humilis,* II M; *D. E. Beetle* 65.
29. *P. Breweri,* I T; *Constance and Morrison* 2191.
30. *P. Fremontii,* II M; *Constance* 2801.
31. *P. ciliata,* I M; *Constance and Beetle* 2535.
32. *P. distans* var. *australis,* II M; *Constance* 2802.
33. *P. ammophila,* I M; *Constance and Killip* 2838.
34. *P. distans,* II M; *Constance* 2563.
35. *P. eximia,* Diak.; *Constance* 2843.
36. *P. malvifolia,* II M; *Constance and Beetle* 2814.
37. *P. lousaefolia,* late Diak.; *Constance* 2840.
38. *P. tanacetifolia,* II M; *Constance and Beetle* 2544.
39. *P. ramosissima,* II M; *Constance and Beetle* 2704.
40. *E. penduliflora,* I M; *Constance and Peirson* 2853.
41. *R. Suksdorfii,* II M; *Constance and Beetle* 2570.

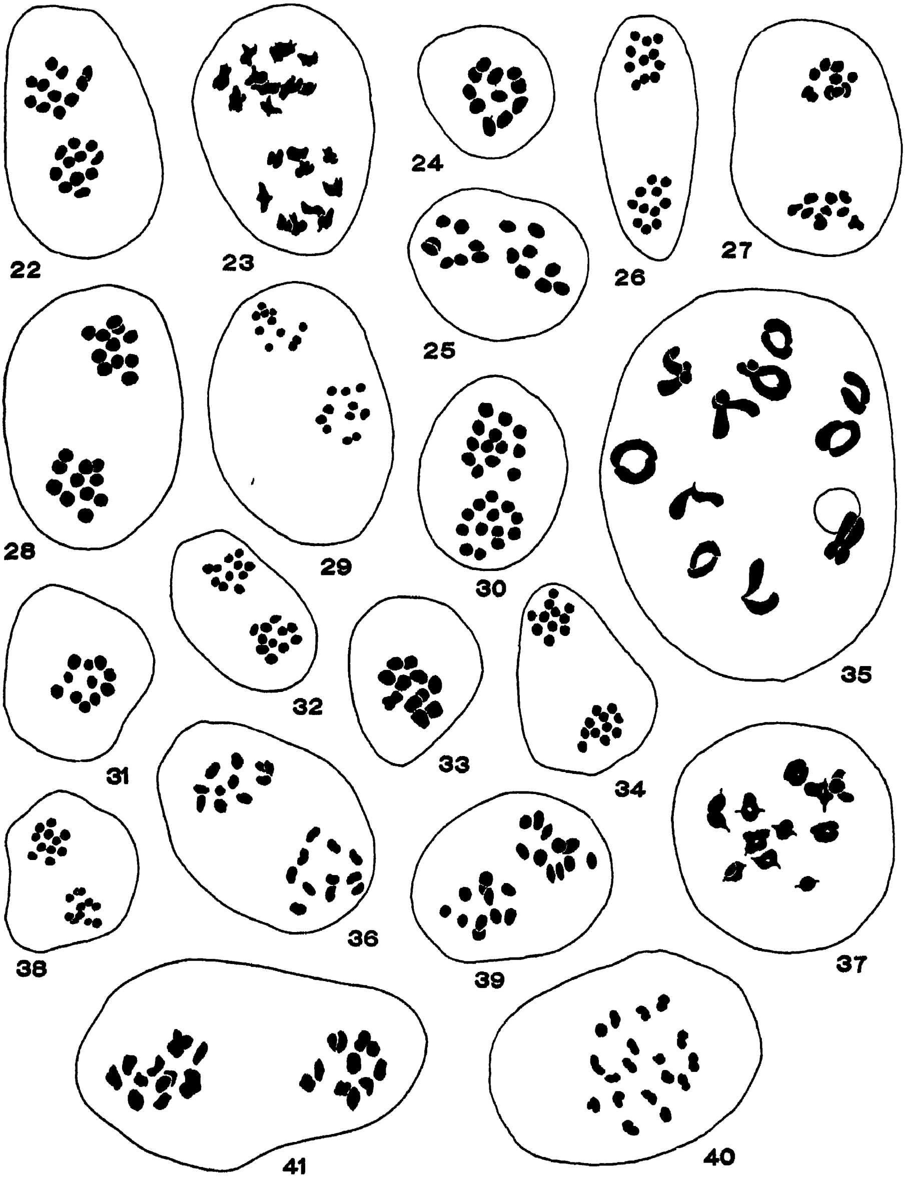

Figure B

Figure C. Chromosomes of the Phacelia magellanica-californica-heterophylla Complex. ×1150.

42. *P. argentea,* II M; *Constance and Beetle* 2625.
43. *P. californica,* II M; *Constance and Beetle* 2609.
44. *P. heterophylla,* Diak.; *Stebbins* 3002.
45. *P. heterophylla,* I M; *Constance* 2829.
46. *P. heterophylla,* Diak.; *Constance and Beetle* 2606.
47. *P. imbricata,* Diak.; *Constance and Peirson* 2846.
48. *P. imbricata,* II M; *Gould and Beach* 1065.
49. *P. imbricata,* II M; *Stebbins* 3071.
50. *P. imbricata,* II M; *Constance* 2839.
51. *P. compacta,* Diak.; *Beach and Mills* 1393.
52. *P. leucophylla,* Diak.; *D. E. Beetle* 67.
53. *P. leucophylla,* II M; *Cave* 4104.
54. *P. mutabilis,* Diak.; *A. A. Beetle* 2778.
55. *P. nemoralis,* II M; *Constance and Beetle* 2674.

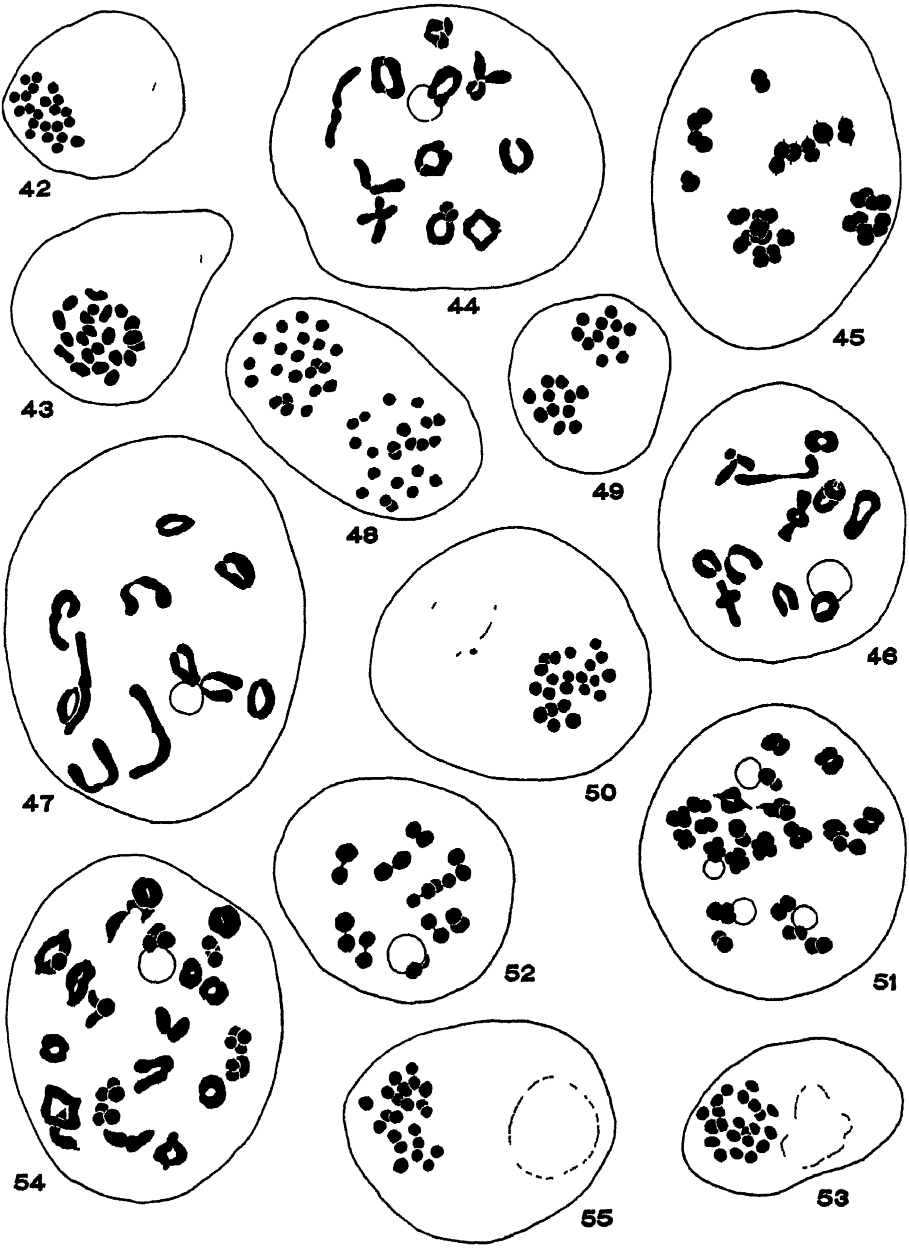

Figure C

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FILICUM NOVARUM CXXVIII DIAGNOSES

BY

EDWIN BINGHAM COPELAND

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FILICUM NOVARUM CXXVIII DIAGNOSES

BY

EDWIN BINGHAM COPELAND

DURING the past four years I have been busy with a monograph of the genus *Grammitis* and with the study of New Guinea ferns, the collections (1) of the Third Archbold Expedition to New Guinea, made in collaboration with the government of the Netherlands Indies, and (2) of Mrs. Mary Strong Clemens. The results are incorporated in the monograph and in ten papers on New Guinea ferns, of which three minor ones have been printed. The remaining papers have been caught by war, in every stage of preparation for publication. Proof has been corrected, returned, and received in Manila, for perhaps half the work; proofs of two papers have been corrected and mailed by me, and returned to me because delivery was impossible; and proofs of some papers I have not received at all. One manuscript, on Mrs. Clemens' latest collections, is held here for a better day.

I do not doubt that the Philippine Journal of Science will resume publication after the liberation of the Philippines; but in the meantime the fate of these papers is unknowable. Under these conditions I am willing to wait indefinitely for their full publication, with full descriptions, plates, changes of name, reductions, extensions of range, and so forth. But the collections, bearing names which have no standing, are distributed to herbaria, and in spite of the general impropriety of preliminary and double publication I feel that the novelties and their names should be protected. For this purpose I have drafted the following diagnoses, sufficient for the purpose, under botanic law.

With the one exception noted, I am the author of all the proposed names and combinations (indicated by boldface type). Except as noted, all novelties are from New Guinea; and except as noted, the type specimens are in my herbarium.

Dicranopteris tomentosa

D. ferrugineae similis, multo densius tomentosa, soris majoribus distincta.

Clemens No. 41238.

Hicriopteris Clemensiae

H. volubili affinis, glabrior, costarum paleis vix 1 mm longis ovatis castaneis sparsis.

Clemens No. 41227.

Meringium laxum

M. dimidiato subsimile majus, pinnis segmentisque paucis remotis, involucro anguste obconico labiis paucidentatis.

Clemens No. 12343-A.

Dicksonia Archboldii

Arbor, rhachibus fuscis setosis, dentibus pinnularum sterilium angustis acutis.

Brass No. 10970.

Orthiopteris trichophylla

O. cicutarioides (Baker, *Davallia*) Copel. (*Ithycaulon tenuisectum* C. Chr.) affinis, fronde angustissime dissecta, segmentis vix 0.3 mm latis.

Brass No. 12057.

Dennstaedtia magnifica

D. rhachibus inermibus setulosis, pinnulis acuminatis, venis inferne setulosis, aliter glabris.

Brass No. 12982.

Lindsaya furcata

Synaphlebium ramis infimis frondis furcatis, pinnulis crenatis, soris marginalibus.

Brass No. 13329.

Hypolepis Archboldii

H. distante affinis, fronde mediocre bipinnata, pinnulis oblongis sparse setosis.

Brass et Myer-Drees No. 9852.

Paesia laevis

P. stipite rhachique nudis laevibus, fronde quadripinnata pinnulis ultimis paucis mediocribus.

Clemens No. 12057.

Lepidocaulon caudatum Copel. gen. et sp. nov.

Histiopteridi affine, fronde bi- tri-pinnata haud rampante, venis nisi in soris liberis.

Brass No. 10714.

Pteris macrophylla

P. tripartita, pinnulis pectinatis, segmentis integris acutis, venis liberis.

Brass No. 10298.

Cheilanthes belensis Weatherby

C. papuanae affinis, stipite paleaceo, lamina coriacea elliptico-lanceolata inferne ceracea, sporis rugosis asperatis.

Brass No. 11212. Type in Herb. Arnold Arb.

Cyathea costalisora

C. paleis stipitis angustis atris brunneo-marginatis, rhachibus perpaleatis costis inferne nudis, soris parvis costularibus indusio truncato.

Brass No. 9488.

Cyathea everta

C. rigenti similis, rhachibus densius paleatis, costis costulisque nudioribus, indusio irregulariter rupto.

Brass No. 10712.

Cyathea bidentata

C. paleis stipitis magnis ochroleucis, rhacheos densis castaneis, fronde quadripinnatisecta lobis bidentatis, indusiis fuscis.

Brass No. 10971.

Cyathea globosora

Arbor alta gracilis C. evertae subsimilis, paleis basalibus nigro-costatis stramineo-marginatis, fronde tripinnata, rhachibus pallide paleatis, indusiis globosis.

Brass No. 10771.

Cyathea pachyrrhachis

C. paleis stipitis rhacheosque crassae muriculatae stramineis deciduis, fronde grande tripinnata, indusiis globosis mox fissis.

Brass No. 12118.

Cyathea quadripinnatifida

C. paleis basalibus longis angustissimis albis nitentibus, fronde longa, pinnulis secundariis auriculatis, indusiis tenuibus persistentibus.

Brass No. 12225.

Cyathea magna

Alsophila stipite spinis paleas fuscas gerentibus horrido, fronde tripinnatifida ampla, costis paleis variis vestitis, soris multis costularibus.

Brass No. 11278.

Cyathea horridula

Alsophila paleis basalibus mediocribus stramineis ciliatis, fronde tripinnatifida, costis deorsum conspicue paleatis.

Brass No. 12043.

Cyathea pilulifera

C. contaminanti affinis, paleis basalibus stramineo-albis flaccidis, fronde mediocre tripinnatifida, venis pilosis.

Brass No. 11192.

Cyathea melanacantha

C. contaminanti affinis, paleis basalibus atrocastaneis nitidis, stipite spinis nigris perhorrido, segmentis laminae varie squamulosis.

Brass No. 9311.

Cyathea gracillima

Thysanobotrya paleis basalibus castaneis aciculatis, fronde tripinnatifida, pinnis dimorphis, pinnulis fertilibus angustis 5 cm longis.

Brass No. 12824.

Cyathea pulcherrima

C. alatae subsimilis, paleis stipitis rhachique castaneo-atris setiformibus, fronde quadripinnatifida herbacea pilosa, soris solitariis indusio persistente.

Brass No. 8940.

Cyathea parva

C. lepidocladae affinis, paleis basalibus stramineis castaneo-aciculatis, fronde parva vix tripinnata, soris squamulis laceris subtensis.

Brass No. 12197.

Cyathea cheilanthoides

C. Macgregori affinis, paleis basalibus longissimis planis castaneis ferrugineo-marginatis, fronde subsessile mediocre tripinnata pinnulis bullatis, indusio persistente.

Brass No. 9283.

Cyathea tomentosissima

C. Macgregori affinis, paleis basalibus castaneis nitidis tortis, fronde parva subtripinnata, pinnulis cucullatis, soris sub tomento denso cinereo exindusiatis.

Brass No. 9116.

Dryopteris spinosa

D. leucolepidi similis, fronde tripinnata, paleis basalibus castaneis ovatis, rhachi puberula spinosa, indusio nullo.

Brass No. 10751.

Dryopteris pulchra

D. vili affinis, fronde quadripinnatifida, stipite setoso-paleaceo, soris ad venas terminalibus.

Brass No. 13455.

Dryopteris speciosissima

D. vili affinis, fronde quinquepinnatifida, stipite setoso-paleaceo, soris ad venas dorsalibus.

Brass No. 11257.

Dryopteris habbemensis

D. viscosae affinis, fronde bipinnata, stipite fusco, rhachibus pubescentibus, lamina glabra.

Brass No. 9304.

Dryopteris platyptera

D. brunneae affinis, fronde subbipinnata, rhachi atropurpurea superne purpureo-strigosa, lamina glabra.

Brass No. 11328.

Dryopteris petrophila

D. philippinae affinis, fronde subbipinnatisecta angusta utrinque attenuata, rhachi pubescente, venis simplicibus.

Brass No. 11326.

Dryopteris Regis

Thelypteris fronde bipinnatifida basi abrupte angustata glabra, pinnis 15 cm longis, indusio inviso.

King No. 496.

Dryopteris subdimorpha

D. crassifoliae affinis, fronde basi truncata, pinnis pinnatifidis basi contractis, soris nudis.

Brass No. 13666.

Dryopteris belensis

D. crassifoliae affinis, pinnis basi rotundatis subcoriaceis 3 cm latis, indusio setuloso.

Brass No. 11509.

Dryopteris ophiura

D. crassifoliae affinis, rhachi pubescente, pinnis paucis caudatis coriaceis, indusio glabro persistente.

Brass No. 12471.

Dryopteris wantotensis

D. crassifoliae affinis, rhachi pubescente, pinnis acuminatis subcoriaceis, indusio glabro persistente.

Clemens No. 11013 bis.

Dryopteris crassa

D. crassifoliae affinis, rhachi inferne glabra, pinnis acuminato-caudatis coriaceis, indusiis nudis fugacibus.

Brass No. 10878.

Dryopteris adenostegia

Cyclosorus, fronde mediocre utrinque angustata setulosa, venis uniparibus anastomosantibus, indusiis glandilis cinctis.

Brass No. 10282. Type in Herb. Arnold Arb.

Dryopteris distincta

Cyclosorus fronde grande basi truncata, pinnis pectinatis, indusio carente, sporangiis setiferis.

Bamler W 11, in Herb. Univ. Calif.

Dryopteris vestigiata

Cyclosorus caudice adscendente, fronde grande basi abrupte contracta setulosa, venis uniparibus anastomosantibus, sporangiis nudis.

Brass No. 12317.

Dryopteris paripinnata

Cyclosorus D. appendiculatae affinis, pinnis subcoriaceis inferne setulosis basi contractis, indusiis sporandiisque nudis.

Brass No. 12435.

Dryopteris deltiptera

D. paripinnatae affinis, pinnis inferne glabris basi dilatatis deinde sensim angustatis.

Brass No. 11260. Type in Herb. Arnold Arb.

Dryopteris subappendiculata

D. deltipterae affinis, pinnis longis basi non dilatatis marginibus parallelis inciso-crenatis.

Brass No. 12247.

Dryopteris multiauriculata

Cyclosorus caudice erecto paleis pubescentibus, fronde grande utrinque angustata superne glabrescente.

Brass No. 12850.

Dryopteris protecta

Cyclosorus caudice erecto paleis puberulentibus, fronde superne glabra, venis biparibus anastomosantibus, indusio setuloso.

Brass No. 10933.

Dryopteris terrestris

Cyclosorus rhizomate brevi-repente paleis setuliferis, fronde mediocre utrinque angustata microscopice setulosa, pinnis abrupte falcato-acuminatis, indusiis sporangiisque setuliferis.

Brass No. 13660.

Dryopteris albosetosa

Cyclosorus paleis atrocastaneis ciliatis, fronde parva utrinque angustata superne setosa, pinnis late lanceolatis.

Brass No. 11435.

Dryopteris strigosissima

D. albosetosae affinis, pinnis inferioribus ad auriculas congestas reductis, indusiis setosis sporangiis glabris.

Brass No. 11434.

Dryopteris riparia

Cyclosorus **D. philippinensi** (Baker, *Nephrodio*) similis, pinnis glabris crassioribus latioribus profundius incisis.

Brass No. 13048.

Dryopteris morobensis

Pseudomeniscium, trunco arboreo, fronde grande subdimorpha, pinnis multis basi cuneato-rotundatis.

Clemens s.n.

Polystichum Archboldii

P. gregis P. aculeati, rhachi inter alias paleis lanceolatis patentibus onusta, pinnulis coriaceis arcte mucronatis.

Brass et Myer-Drees No. 9850.

Polystichum muticum

P. gregis P. lobati, pinnulis oblongis rotundatis integris vel crenatis.

Brass No. 11434.

Polystichum Myer-Dreesii

P. mutico affine, pinnulis incisis vel subpinnatis.

Brass et Myer-Drees No. 10033.

Polystichum cheilanthoides

Papuapteridi affine vel congenericum, fronde ampla subtripinnata haud stricta, pinnulis bullatis.

Brass et Myer-Drees No. 9801.

Papuapteridis forman misit relicta Clemens quam typico minus strictam, paleis pro parte vetustate dejectis. Genus ad lib. aut conservandum aut Polysticho reducendum.

Tectaria pubescens

T. ferrugineae affinis, fronde minus dissecta, ideoque serie altera areolarum distincta, indusiis persistentibus.

King No. 359 (quondam T. malayensis appellata).

Athyrium minutum

Nanum A. setifero affine lamina tripinnatifida, soris basalibus brevibus indusio lato.

Brass et Myer-Drees No. 10107.

Athyrium Myer-Dreesii

A. setifero affine, fronde mediocre subtripinnata pinnis acuminatis, indusio lato recto.

Brass et Myer-Drees No. 9851. Type in Herb. Arnold Arb.

Athyrium latilobum

A. sylvatico affine, fronde grande tripinnata, rhachi furfuracea, pinnis secundariis integris herbaceis.

Brass No. 13420.

Athyrium pedicellatum

A. latilobo affine, minus, tripinnata, rhachi glabra sed nodis paleis solictariis praeditis.

Clemens No. 41566.

Athryium decompositum

Brachysorus fronde grande tripinnata papyracea, pinnulis secundariis incisis, soris costularibus brevibus.

Bamler No. 128 (1914). Type in Herb. Univ. Calif.

Athyrium Archboldii

A. rhacheos fuscae paleis nigris rigidis, pinnis 6 cm latis profunde pinnatifidis.

Brass No. 12272.

Blechnum Brassii

Lomaria rhizomate scandente, fronde basi truncata, pinnis liberis acutis basi rotundatis integris 6 cm longis.

Brass No. 12287.

Blechnum nudius

B. fluviatili affine, rhachi sparsissime paleacea vel nuda, textura firmiore distinctum.

Brass et Myer-Drees No. 9966.

Asplenium morobense

Micropodium fronde mediocre longe stipitata utrinque angustata glabrescente haud prolifera, venis liberis.

Clemens No. 41541.

Asplenium durum

Fronde simplice sessile rigide coriacea parva, venis liberis immersis.

Brass No. 11639.

Asplenium Clemensiae

Nanum gregis A. insititii, fronde subbipinnata, rhachi prolifera; adspectu *A. gracilis* Fée nec Don, quod *A. planicaulis* Wall. nec Lowe forma nana est.

Clemens No. 41740.

Asplenium paedigens

Euasplenium adspectu Dareae, proliferum, fronde tri- quadri-pinnata segmentis 1 mm latis cuneiformibus.

Brass No. 12896.

Lomagramma angustipinna

L. frondis sterilis pinnis linearibus herbaceis venis inconspicuis, sporangiis purpurascentibus.

Brass No. 13446. Type in Herb. Arnold Arb.

Grammitis nudicarpa

G. Wattsii (*Polypodio pulchello* Watts nec aliorum) affinis, minor, paleis ciliatis, soris a costa remotis.

Type in Herb. Lugd. Bat., No. 908,302 . . . 93. Lord Howe Ins.

Grammitis neocaledonica

G. Reinwardtii similis, paleis occultis, fronde dense longeque setosa venula fertile brevissima, sporangiis setulosis.

Schlechter No. 15346. Type in Herb. Lugd. Bat. Nova Caledonia.

Grammitis insularis

G. conformi affinis, venis bis furcatis, soris inframedialibus conspicue immersis.

Vaupel No. 451. Type in U. S. Nat. Herb. Samoa.

Grammitis caricifolia

G. frigidae (Ridley, *Polypodio*) affinis, stipite longa glabrescente, lamina paullo longiore coriacea glabra.

Clemens s.n.

Grammitis graminifolia

G. fasciatae affinis, frondibus angustissimis (3 mm latis) marginibus nigro-setulosis venis hic illuc anastomosantibus.

Brass No. 5092. Type in Herb. N. Y. Bot. Gard.

Grammitis plurisetulosa

G. loculosae (v.A.v.R., *Polypodio*) affinis, paleis stramineis, stipitibus longis, sporangiis setulis pluribus ornatis.

Brass et Myer-Drees No. 10109.

Grammitis ceratocarpa

G. plurisetulosae affinis, paleis fuscis ovatis, stipitibus sparse setosis, lamina opaca.

Clemens No. 11349.

Grammitis dictymioides

G. loculosae affinis, frondibus anguste linearibus, venis saepe anastomosantibus, crateris sororum ciliatis.

Brass No. 11848.

Grammitis stomatocarpa

G. locellatae (Baker, *Polypodio*) affinis, fossis sororum linearibus diutius clausis.

Brass et Myer-Drees No. 9858-A.

Grammitis novoguineensis

G. scabristipedi (Baker, *Polypodio*) affinis, basibus setarum bulbosis, soris superficialibus elongatis subirregularibus.

Bamler No. B. 41. Type in Herb. Univ. Calif.

Grammitis Mariae

G. stipitibus dense setosis, lamina inciso-crenata setosa, venis praestantibus, venula fertile breve, sporangiis setuliferis.

Clemens No. 10251-A.

Grammitis matapensis

G. Reinwardtii affinis, lamina membranacea, venis sterilibus simplicibus, setis sporangiorum longis.

Clemens No. 11176.

Grammitis brevisetulosa

G. paleis ferrugineis cellulis maximis, pilis stipitum fuscis 1 mm longis, soris ad venulas elongatas basalibus.

Clemens, cum *No. 40969* mixtum.

Grammitis debilifolia

G. fasciculatae affinis, frondibus pendentibus anguste oblanceolato-linearibus, venis costae fere parallelis.

Brass et Myer-Drees No. 10036.

Grammitis Myer-Dreesii

G. fasciculatae affinis, stipitibus longis sparse pilosis, lamina sparsissime setosa, venulis fertilibus elongatis, sporangiis dense setosis.

Brass et Myer-Drees No. 9898.

Grammitis habbemensis

G. fasciculatae affinis, gracilius et densius hirsuta, soris ad venulas elongatas suprabasalibus.

Brass No. 10520.

Grammitis trogophylla

G. mollipilae (Baker, *Polypodio*) affinis, fronde parva densissime setosa, sporangiis deciduo setiferis.

Clemens s.n. Eadem species est *Clemens No. 10087.*

Grammitis cyclosora

G. trichopodae (Mueller et Baker, *Polypodio*) similis, rhizomate erecto, venis semel furcatis venulis elongatis.

Clemens s.n.

Grammitis nigropaleata

G. trichopodae affinis, setis ubique longioribus, praecipue paleis parvis nigris distincta.

Clemens No. 41018.

Grammitis hispida

G. knutsfordianae (Baker, *Polypodio*) affinis, rhizomate longe repente, lamina minute dense rigide setulosa.

Brass No. 10257.

Grammitis Fenicis

G. dorsipilae (Christ, *Polypodio*) similis, G. congenerae affinior, setis saepe fasciculatis, venis bis furcatis.

Bu. Sci. (*Ramos*) *No. 80147.* Batanes Ins.

Grammitis Holttumii

G. hirtellae (Blume, *Polypodio*) affinis, major, brevius stipitata, setis 3 mm longis ubique densis distincta.

Holttum No. 23384. Malaya Peninsularis.

Grammitis peninsularis

G. hirtellae affinis, fronde pusilla ubique setulis nigrescentibus brevissimis dense obsita.

Holttum No. 20678. Malaya Peninsularis.

Grammitis nigrosetosa

G. setosae affinis, setis frevioribus densis nigris, venis bis furcatis, soris partim irregulariter sparsis.

Stresemann No. 404. Buru. Type in Herb. Lugd. Bat.

Grammitis Stresemannii

G. setosae affinis, stipite densissime setoso, soris ad laminam inframedialibus, ad venulas apicalibus.

Stresemann No. 268. Ceram. Type in Herb. Lugd. Bat.

Grammitis marivelesensis

G. fasciculatae affinis, stipite pilisque brevioribus, fronde angustiore herbacea haud spongiosa distincta.

Copeland No. 215. Mt. Mariveles, luzonensem.

Xiphopteris antipodalis

X. rhizomate breve erecto, frondis parte sterile pinnata, rhachi inconspicue alata.

Brass No. 10788.

Calymmodon grammitidiphyllus

C. fronde simplice deorsum integra, sursum lobis fertilibus more generis conduplicatis leviter incisa.

Brass No. 13443.

Calymmodon ramifer

C. fronde ramifera, pinnis minutis oblongis herbaceis, fertilibus basi contractis.

Brass et Myer-Drees No. 9943-A.

Calymmodon fragilis

C. fronde crassa fragile, rhachi filiforme, pinnis fertilibus permultis ovatis basi contractis.

Brass et Myer-Drees No. 10035.

Ctenopteris beleensis

C. fronde anguste lineare debile herbacea lanosa, pinnis triangulari-oblongis integris.

Brass No. 11041.

Ctenopteris schizophlebia

C. paleis integris, fronde pinnatifida papyracea, segmentis angustatis acutis integris, venis plerisque furcatis.

Clemens s.n.

Ctenopteris Clemensiae

C. schizophlebiae affinis, segmentis lineari-oblongis obtusis vel rotundatis distincta.

Clemens s.n.

Ctenopteris integripaleata

C. stipite basi paleato paleis integris, fronde subpinnata basi abrupte contracta coriacea, venis fertilibus furcatis, soris superficialibus.

Brass No. 12249.

Ctenopteris rawlinsonensis

C. paleis ciliatis linearibus, stipite glabrescente, pinnis erecto-patentibus angustis acuminatis integris glabris, soris superficialibus.

Clemens No. 41953.

Ctenopteris rhodocarpa

C. nutanti affinis, segmentis approximatis anguste confluentibus glabris, venis confertis permultis.

Clemens s.n.

Ctenopteris pubipes

C. rhodocarpae affinis, stipitibus setosis, venis paucis remotis distincta.

Clemens s.n.

Ctenopteris fusca

C. nutanti affinis, ob frondem valde decurvam, pinnasque retroflexas et dorso ad dorsum imbricatim appressas mirabilis.

Brass et Myer-Drees No. 9897.

Ctenopteris stellatosetosa

C. **celebicae** (Blume, *Polypodio*) affinis, setis conspicue fasciculatis distincta, pinnis latioribus, soris minus appressis.

Clemens No. 40959.

Ctenopteris venulosoides

C. venulosae affinis, stipite longo, receptaculis ellipticis costae parallelis crateris haud ciliatis.

Clemens No. 41394.

Ctenopteris Brassii

C. **Ledermanni** (Brause, *Davalliae*) affinis, pinnarum basibus subauriculato-adnatis haud confluentibus distincta, crateris ciliatis.

Brass No. 9302.

Ctenopteris sesquipinnata

C. **bipinnatifidae** (Baker, *Polypodio*) affinis, non ramosa, pinnis pinnatifido-serratis glabrescentibus, soris costalibus.

Brass No. 9510.

Ctenopteris polytricha

C. bipinnatifidae affinis, fronde densissime pilosa, pinnis pinnatifido-lobatis, soris lobos complentibus.

Brass No. 10518.

Ctenopteris bipinnata

C. bipinnatifidae affinis, frondibus longissimis angustissime dissectis, rhachibus filiformibus, pinnulis minutis.

Brass No. 9433.

Prosaptia Archboldii

P. contiguae affinis, fronde pinnata, setis saepe binatis vel ternatis distincta.

Brass No. 12020.

Cyclophorus Brassii

C. indumento appresso paleis pallidis stellatis radiis sex ad octo, soris magnis conspicue immersis.

Brass No. 11372.

Elaphoglossum habbemense

Nanum E. laurifolio affine, paleis ferrugineis subciliatis, frondis sterilis stipite 25 mm longo, fronde rigida glabrescente.

Brass No. 9083. Type in Herb. Arnold Arb.

Elaphoglossum Archboldii

E. callifolio affine, paleis fuscis minutis, frondibus fasciculatis, sterile longe decurrente glabrescente.

Brass No. 13220.

Elaphoglossum brunneum

E. paleis atris minutis angustis, frondibus remotis oblanceolatis basi cuneatis vix decurrentibus atrosquamulosis.

Brass No. 12808. Type in Herb. Arnold Arb.

Elaphoglossum repens

E. rhizomate gracile, frondibus late oblanceolatis rotundatis basi breviter decurrentibus glabrescentibus.

Brass No. 12124.

Elaphoglossum fuscum

E. rhizomate repente crasso, paleis magnis nigrescentibus ciliatis, frondibus oblanceolatis rotundatis basi cuneatis, squamulis variis.

Brass No. 9088.

Elaphoglossum laticuneatum

E. fusco affine, frondibus remotis, sterile late oblongo-spatulata minute squamosa, fertile conforme.

Brass et Myer-Drees No. 10032.

Goniophlebium subcordatum

G. paleis parvis densis appressis, pinnis glabris, basi subcordatis non dilatatis, soris superficialibus.

Brass No. 14015.

Goniophlebium subimpressum

G. pinnis basi suboblique rotundato-cuneatis subcoriaceis glabris, soris vix immersis.

Clemens No. 41232.

Polypodium crassimarginatum

Crypsinus, P. gracilipedi affinis, paleis margine minute denticulatis, fronde sterile elliptica, fertile lineare, soris superficialibus.

Brass No. 13225.

Oleandropsis, gen. nov.

Genus Crypsino derivatum caudice rampante, frondibus polytaxicis simplicibus dimorphis, soris elongatis confluentibus.

Type: **O. ferrea** (Brause, *Polypodium*). *Grammatopteridi* sp. C. Chr.

Selliguea brachylepidota

S. Feei affinis, paleis maximis fulvis appressis late imbricatis, soris plerisque interruptis.

Clemens No. 41008.

Merinthosorus Hieronymi

M. Thomsoni (Baker, *Acrosticho*) affinis, fronde stipitata profundius pinnatifida, costis conspicue pubescentibus.

Brass No. 11700. An *Dryostachyum Hieronymi* Brause?

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IN THE COURSE of our investigations on various genera in this tribe of the Compositae it has become necessary to transfer certain species from one genus to another. Several of these species have generally been accepted in the genus *Crepis* for many years, and it is desirable to publish these transfers in advance of publication of the now nearly completed monograph on that genus.

The abbreviations indicating herbaria in which specimens are cited are as follows:

B, Berlin, Herbarium of the Botanical Museum, University of Berlin
Bur, Burnat Herbarium in the De Lessert Herbarium, Geneva
Cal, Calcutta, Herbarium of the Calcutta Botanic Garden
DD, Dehra Dun, Herbarium of the Forest Research Institute and College, Dhera Dun
E, Edinburgh, Herbarium of the Royal Botanic Garden, Edinburgh
Fl, Florence, Herbarium of the Botanical Institute, University of Florence
G, Gray Herbarium of Harvard University
HU, Herbarium of the Hebrew University, Jerusalem
K, Kew, Herbarium of the Royal Botanic Gardens, Kew
Lenin, Leningrad, Herbarium of the Principal Botanic Garden, Leningrad
Ms, Montpellier, Herbarium of the Institute of Botany, University of Montpellier
MW, Wien, Naturhistorisches Museum, Vienna
O, Oxford, Herbarium of G. C. Druce, Oxford University
UC, University of California, Herbarium of the University of California, Berkeley
US, United States National Herbarium, Washington, D. C.

I. THE GENUS YOUNGIA

At the time of publication of the monograph on *Youngia*[1] there were four species which were doubtfully accepted in *Crepis*, but which were not then sufficiently known to justify their exclusion. More recently additional material of the first two described below has become available and, on the basis of this evidence, their transfer to *Youngia* is justified. On the strength of this decision and from a reëxamination of the available material, the transfer of the other two species to *Youngia* also seems to be warranted. It has been possible to place each of these four species in one of the sections of *Youngia* (cf. Babcock and Stebbins, *op. cit.*).

Youngia setigera (Scott) comb. nov.

(Figure 1)

Perennial, 1–2 dm. high, with vertical caudex over 4 cm. long, 6–8 mm. wide, covered with black bases of old leaves, brown-woolly at base of leaves; caudical leaves few, ascending, up to 12 cm. long, 3.5 cm. wide, narrowly elliptic, acute or acuminate, coarsely and irregularly runcinate-dentate, segments triangular, ± retrorse and mucronate, attenuate into a stout winged petiole ¼–⅜ as long as blade with clasping base, rather thick, dark above and pale beneath, margin retrorsely revolute, conspicuously setose beneath, on petiole, midrib and veins, less so above, with long dark purple glandless bristles; cauline leaves similar, short petioled or sessile, sometimes caudate-acuminate with acuminate teeth, uppermost 1–3 cm. long; stem stout, erect or curved, branched at the top to form a dense 9–16-headed compound corymbiform cyme, sometimes with 2–3 short few-headed branchlets lower down, striate, like the peduncles conspicuously setose with purple glandless bristles; peduncles short, ± fuscous-tomentose; heads erect, 9–13-flowered; involucre cylindric 10–11 mm. high, 2.5–3 mm. wide at receptacle, ±setose; outer bracts 5–7, unequal, 0.5–2.5 mm. long, lanceolate, acute, dorsally setose; inner bracts 7–8, lanceolate, obtuse, innermost membranous-margined, ventrally glabrous or with a few minute appressed white hairs, dorsally beset with a median row of the characteristic long purple glandless setae, becoming carinately spongy-thickened near base; receptacle alveolate-fimbrillate, alveolae irregularly pentangular, 0.4 mm. wide, fimbrillae low, thick, waxy, glabrous; corolla yellow, 12 mm. long; ligule 2 mm. wide; teeth 0.8 mm. long; corolla tube 2.5 mm. long, glabrous except a few short several-celled trichomes; anther tube 5 × 1.5 mm. when opened out; appendages 0.8 mm. long, obtuse; style-branches 2 mm. long, 0.1 mm. wide, black in sic., stigmatic face yellow; achenes pale or dark brown, darker at the apex, 4.5–5.5 mm. long, 0.75 mm. wide at middle, gradually attenuate to the apex which is 0.3–0.5 mm. wide, with slightly expanded

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[1] Babcock, Ernest B. and G. Ledyard Stebbins, Jr. The Genus Youngia. Carnegie Inst. Wash. Publ. No. 484. 1937.

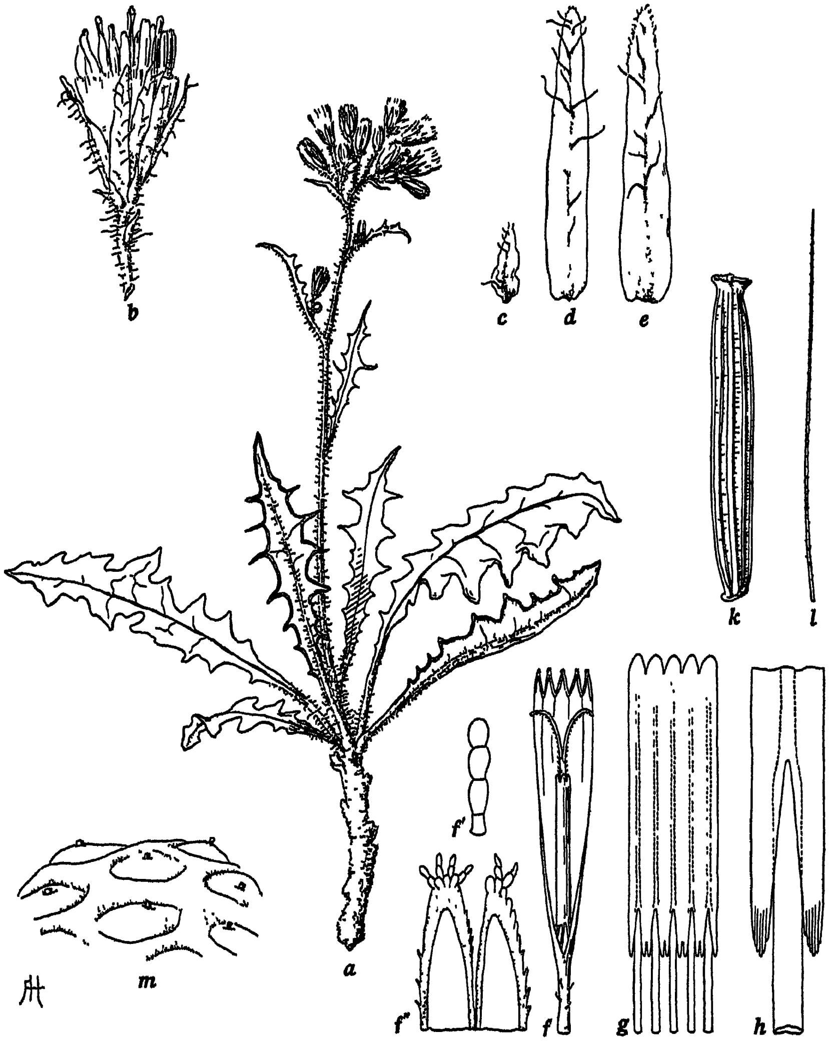

Fig. 1. *Youngia setigera*, from type and isotype; *a*, plant, ×½; *b*, young head, ×2; *c*, *d*, *e*, one outer and two inner involucral bracts, dorsal view, × 4; *f*, floret, lacking ovary, × 4; *f*′, trichome from corolla tube, × 16; *f*″, detail of ligule teeth, × 25; *g*, anther tube, × 8; *h*, detail of appendages, × 32; *k*, *l*, achene and a pappus bristle, × 8; *m*, detail of receptacle, × 25.

pappus disk, abruptly narrowed above the small calloused hollow base, about 12-ribbed, ribs unequal, 4–5 very prominent, rounded, smooth; pappus 5–7 mm. long, pale brown, 1-seriate, coarse, brittle, densely barbellulate, persistent. Flowering July–Sept.; flowers yellow. (*Crepis setigera* Scott ex W. W. Smith, Notes Bot. Gard. Edin. 8:333. 1915.)

Western China in western Szechwan and southwestern Yunnan.

CHINA: Szechwan, mountain pastures of Tcha-ho, 2600 m., *E. E. Mawe 72, type, 197,* (E); Yunnan, Laingshan Mts., Chio-kia Hsien, open grassy slope, *Tsai 52022* (G).

Youngia setigera is a unique species, having no very close relatives. The elongated woody caudex suggests a primitive type, and the achenes are not specialized. The available achenes are not quite fully mature, but without question, four or five of the ribs are much stronger than the others. This species shows the closest connection with *Y. paleacea* and three other species comprising the second subgroup in Sec. Mesomeris (cf. Babcock and Stebbins, Carnegie Inst. Wash. Publ. No. 484:26, 59. 1937). It resembles that subgroup in habit, leaf shape, and the revolute margins of the leaves, in the narrow, few-flowered involucres, the areolate receptacle, and in the shape and ribbing of the achenes. It differs from them however, in the absence of tubercles on the involucral bracts, the conspicuous purple setae on stems, leaves and involucres, the black styles, and the light brown, rather brittle pappus; also from all but one of those species in the yellow anther tube. *Y. setigera,* therefore, must be placed in a subgroup by itself in Sec. Mesomeris; and because of its strong woody rootstock and brown, brittle pappus, it may be considered the most primitive subdivision of that section.

Youngia racemifera (Hook. f.) comb. nov.

(Figure 2)

Perennial, 1.5–5 dm. high; root horizontal, oblique or vertical, 1–3 cm. long, 0.5 cm. wide, prolonged into a slender taproot or branched, bearing fine fibers; caudex short, 0.5 cm. wide, stoloniferous (?); early caudical leaves ephemeral, 1–3 cm. long, spatulate, ovate, obtuse or acute, constricted into a filamentous petiole; later caudical and lower cauline leaves 3–8 cm. long, up to 3 cm. wide, spatulate, ovate to ovate-lanceolate, acute or acuminate, blade cordate or rounded and constricted into a slender petiole equal to or longer than the blade, sinuate-denticulate, sometimes 4-5-angled, glabrous or puberulent on the upper face, upper leaves lanceolate and short-petioled, or linear and sessile, or bractlike; stem slender, erect, sinuate or strongly curved at base, terete, striate, glabrous, simple or paniculately 3–4-branched, branches 1–24 cm. long, remote, strict, racemiform; peduncles very short, erect, curved at summit in anthesis, bracteate; heads half-nodding, medium, 10–25-flowered, erect in bud, horizontal or drooping in anthesis; involucre campanulate, 10–13 mm. long, glabrous; outer bracts 8, unequal, longest ¼–⅓ as long as inner bracts, lanceolate, acute; inner bracts 8–10, linear, obtuse or acute, yellow-ciliate at tip, very thin, sometimes faintly keeled dorsally but otherwise unchanged in fruiting heads; corolla 17 mm. long; ligule 2.5 mm. wide; teeth 0.75 mm. long, acute; corolla tube about 8 mm. long, glabrous; anther tube 4.5 × 1.25 mm. when opened out; appendages 1 mm. long, narrow, acuminate; filaments stout, 2 mm. longer; style 2.5 mm. wide, extruded 4 mm. beyond anther tube, style-branches exceeding ligule, 2 mm. long, 0.15 mm. wide, strongly attenuate at tip, dark green or black, yellow on inner face; achenes subcompressed, oblong or slightly broader above the middle, constricted at the apex, with expanded pappus disk and hollow base, 12–14-ribbed, the ribs very unequal with 3–5 much stronger; pappus yellow or tawny, about 8 mm. long, copious, 2-seriate, rather fine, somewhat brittle, persistent. Flowering Aug., Sept.; flowers yellow with darker ligule teeth; styles well extruded, black or dark green; corolla tube nearly equal to ligule. (*Crepis racemifera* Hook. f., Fl. Brit. Ind. 3:307. 1882; *Hieraciodes racemiferum* O. Kuntze, Gen. 1:346. 1891; *Crepis rapunculoides* Dunn, Jour. Linn. Soc. 35:512. 1903.)

Eastern Himalaya region eastward to northwestern Yunnan and western Szechwan (Sikang) from 2400 to 4150 m. alt., cold temperate and alpine zones; forests and grass lands.

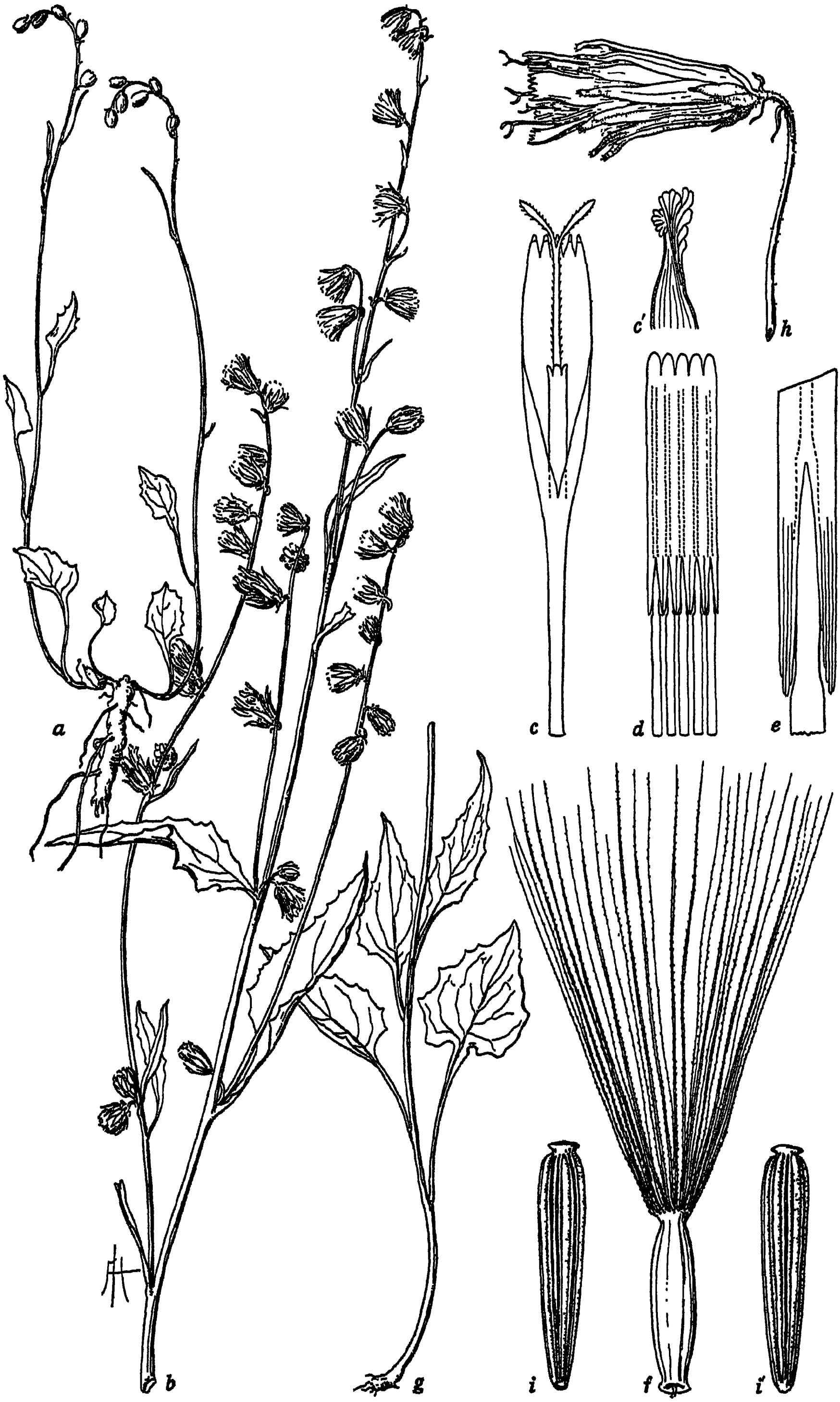

Fig. 2. *Youngia racemifera*, *a–f*, from type; *g*, from *Gammie 1022* (Cal); *h*, from *Pratt 449* (K); *i*, *i′* from *Wang 69972* (G): *a*, small plant, × ½; *b*, upper portion of a large plant, × ½; *c*, floret lacking ovary, × 4; *c′*, detail of ligule tooth, × 25; *d*, anther tube, × 8; *e*, detail of appendages, × 32; *f*, immature achene with pappus, × 8; *g*, lower portion of a medium sized plant, × ½;

British India: Sikkim, Luchoung (Lachung), 2424 m., *J.D.H. 6* (K) type; *ibid.*, 2424–3939 m., *J.D.H. 6* (K) isotype; Sikkim, Thangu, *Prain* in 1903 (K, DD); Sikkim, Lachung, 3030 m., *Gammie 1022* (Cal); Yamphing, 3000 m., *Ghose* in 1930 (UC). China: Yunnan, near Tibetan frontier, 28° 15′ N., Mt. Dokerla, 2800–4150 m., among *Abies* and *Salix*, *Handel-Mazzetti 7246* (MW); Yunnan, A-tun-tze, 2700–3000 m., *Wang 69739, 69877, 69972* (G); Szechwan, 27° 48′ N., Mt. Kwanghang-dse, between Yenyuen and Kwapi castle, in grass, 3900–4075 m., *Handel-Mazzetti 5519* (MW); Szechwan, Tibetan frontier, chiefly near Tatsienlu, 2727–4090 m., *Pratt 449* (K) as *Crepis rapunculoides* Dunn; Szechwan (Sikang), Gue-sai-gue, Tsa-wa-rung, 3200 m., *Wang 65807* (G); Sikang, Chi-na-tung, Tsa-wa-rung, 2800 m., *Wang 65214, 65352* (G).

Youngia racemifera somewhat resembles *Dubyaea hispida* (Don) DC., in habit and leaf shape; and the broad, flat style-branches are suggestive of this genus as well as of *Prenanthes*, of which some species have an inflorescence similar to that of *Y. racemifera*. In the characters mentioned above it shows less resemblance to *Youngia silhetensis* (DC.) Babc. and Stebbins, although Hooker (*loc. cit.*) expressed the opinion that it is very near *Y. silhetensis;* but in type of involucre and nature of the pappus *Y. racemifera* does approach certain other primitive species of *Youngia*, especially *Y. depressa* and *Y. conjunctiva*. The closest resemblance, however, is found in *Y. stenoma* and this resemblance is not restricted merely to habit of the plant and the racemose inflorescence. Certain floral characters are also strikingly similar, particularly the relatively long, glabrous corolla tube and the narrow, conspicuously crested apices of the ligule teeth. The involucres are also similar in the two species except for the absence of tubercles on the inner bracts in *Y. racemifera*. The achenes are also similar both as to size and shape as well as in number and unequal width of the ribs; but the yellowish, brittle, persistent pappus of *Y. racemifera* is very different from that of *Y. stenoma*. On the whole, there is sufficient resemblance to *Y. stenoma* to warrant the classification of *Y. racemifera* in the same section, Stenophytum (cf. Babcock and Stebbins, Carnegie, Inst. Wash. Publ. 484:25, 42. 1937).

Youngia serawschanica (B. Fedtsch.) comb. nov.

(Figure 3)

Perennial, 1.5–2.4 dm. high; caudex elongated from a slender woody rootstock, simple or divided, brown-scaly, 4 mm. wide at the leafy crown; caudical leaves up to 7 cm. long, 2 cm. wide, oblanceolate, acute or caudate-acuminate, denticulate to runcinate-pinnatifid or pinnately parted with triangular or linear acute segments, attenuate into a winged petiole with broader clasping base, glabrous or glaucous, corneous-mucronate, midrib pale; lower cauline leaves similar or sessile; middle and upper cauline leaves much reduced or bractlike; stems 1–2, dichotomously branched from near base, branches few, remote, divaricate or arcuate, slender, striate, glabrous, few-headed; peduncles 0.5–5 cm. long, arcuate, glabrous or slightly tomentulose; heads erect, narrow, 4–6-flowered; involucre cylindric, 12–13 mm. long, 3 mm. wide in anthesis, glabrous, slightly tomentulose at base, or with a few pale glandless hairs near the apex of inner bracts; outer involucral bracts 5–6, unequal, longest ⅕–⅓ as long as inner bracts, ovate to lanceolate, entire or laciniate, shortly ciliate at the apex and with a small black dorsal tubercle near the apex; inner bracts 5–6, lanceolate, acute or obtuse, dorsally tuberculate or corniculate near the apex, somewhat carinate near the base in anthesis, glabrous on both sides or with a few dorsal hairs near the apex; corolla 17–19 mm. long; ligule 3–3.5 mm. wide; ligule teeth 0.4–0.6 mm. long; corolla tube 3 mm. long, very stout, glabrous; anther tube 6.25 × 2 mm. when opened out; appendages 0.8 mm. long, oblong, obtuse with indented apex; filaments stout, about 1 mm. longer; style-branches 3.5 mm. long, 0.3 mm. wide, attenuate at the apex, yellow; achenes (very immature) fusiform, compressed, constricted at summit, with expanded pappus disk, obscurely unequally ribbed; pappus 6–7 mm. long, tawny or pale brown, 2-seriate, setae rather coarse,

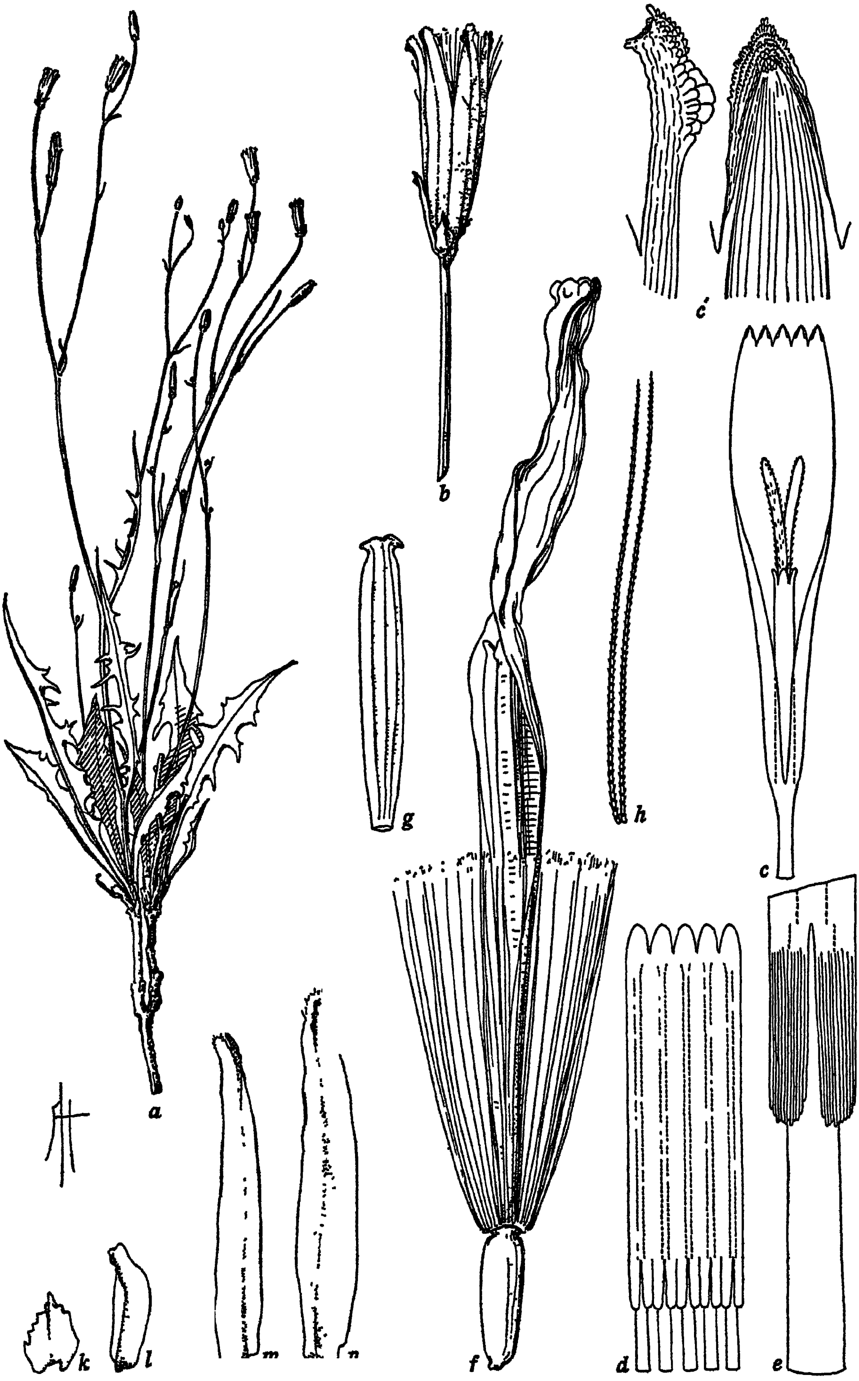

Fig. 3. *Youngia serawschanica*, from *Komarov* in 1892 (Lenin): *a*, plant, × ½; *b*, head, × 2; *c*, floret lacking ovary, × 4; *c′*, detail of ligule teeth, × 25; *d*, anther tube, × 8; *e*, detail of appendages, × 32; *f*, floret with ovary and pappus, × 4; *g*, immature achene, × 8; *h*, section through the 2-seriate pappus, × 8; *k*, *l*, outer involucral bracts, × 4; *m*, *n*, inner involucral bracts, outer face, × 4.

finely barbellulate, barbels ± brown-pigmented giving a speckled appearance en masse in some heads. Flowering June–Aug.; flowers yellow, purplish on outer face of ligules. (*Crepis serawschanica* B. Fedtsch., Beih. Bot. Centralbl. 40:203. 1923.)

Eastern Turkestan, between Bokhara and Samarkand, "Serawschan" (= Zarafshan Mts., presumably), 1800–2700 m. alt. Of the two specimens seen by the authors and cited below, the first is cited first in the original description and may be considered as the type (cf. fig. 3*a*). In addition to these citations, the following localities are mentioned by Fedtschenko: Dorf Chairambet, Pass Puschchin, Pass Dukdon, Langlif, Roch, all collected by Komarov. There are no ecological observations.

TURKESTAN: Seravschan, Voru, *Komarov* in 1892 (Lenin) type; Mura Pass, *Komarov* in 1892 (Lenin).

Youngia serawschanica is very close to *Y. distincta* but it is probably a different species (cf. p. 235). Both are certainly close to *Y. tenuifolia* and may therefore be classified under Sec. Crepidopsis (cf. Babcock and Stebbins. Carnegie Inst. Wash. Publ. No. 484:25, 46. 1937).

Youngia distincta (Popov et Vved.) comb. nov.

(Figure 4)

Perennial, 1.7–2.5 dm. high; caudex elongated from a slender woody rootstock, simple or divided, brown-scaly, 4–5 mm. wide at the leafy crown; caudical leaves up to 11 cm. long, 2.5 cm. wide, oblanceolate, acute or caudate-acuminate, runcinate-dentate to pinnately parted with linear acute segments, attenuate into a winged petiole with broader clasping base, glabrous or glaucous, corneous-mucronate, midrib pale; lower cauline leaves similar or sessile; middle and upper cauline leaves much reduced or bractlike; stem erect, dichotomously branched from near base, branches few, remote, divaricate or arcuate, slender, striate, glabrous, few-headed; peduncles 0.5–7 cm. long, striate, glabrous or sparsely tomentulose; heads erect, about 9-flowered; involucre cylindric-campanulate, 11–12 mm. long, 3–4 mm. wide in anthesis, pubescent with pale setiform hairs; outer bracts 5, nearly equal, ⅕–¼ as long as inner bracts, ovate, acute or obtuse, glabrous or pubescent, ± thickened dorsally near the apex; inner bracts 8, lanceolate, obtuse, shortly ciliate and dorsally tuberculate near the apex, finely carinate dorsally in anthesis, with a median row of yellowish mostly glandless hairs, glabrous on inner face; corolla 17–18 mm. long; ligule 3.5 mm. wide; ligule teeth 0.6–0.75 mm. long; corolla tube 4 mm. long, very stout, glabrous; anther tube 5 × 2 mm. when opened out; appendages 0.75 mm. long, oblong, acute or obtuse; filaments about 0.5 mm. longer, stout; style-branches 3 mm. long, 0.25 mm. wide, yellow; achenes (very immature) fusiform, compressed, constricted below expanded pappus disk, obscurely ribbed with 3 stronger ones evident on one side; pappus 7 mm. long, tawny or pale brown, 4-seriate, setae rather coarse, finely barbellulate, barbels ± brown-pigmented giving a speckled appearance en masse. Flowering July; flowers yellow, purplish on outer face of ligule. (*Crepis distincta* Popov et Vved., Bull. Soc. Nat. Mosc. n.s., 42:128, 147. 1933.)

Eastern Turkestan, western Tian-Shan Mts., north of Samarkand, from 1000 to 3500 m. alt. The following observations are from Pavlov (*loc. cit.*):

"Apparently it is endemic in the western Tian-Shan, where the plant is known from the south up to Chimgan and from the east up to the Chatkal range. We encountered it only in the Talass-Alatau where it occurred in the lower zones from 1000 to 3000–3500 meters of absolute altitude. The plant is small and insignificant and occurs singly and scattered in the meadow associations on the mountain slopes and plateaus."

In addition to the type specimen, cited below, Pavlov lists the following locality: Czimgan Major Mts., alpine region.

TURKESTAN: Talass-Alatau Mts., rocky slopes, headwaters of Dshebogly-su (Toptchak-su [?]) R., 2000 m., July 20, 1931, *Pavlov 658* (Lenin) type.

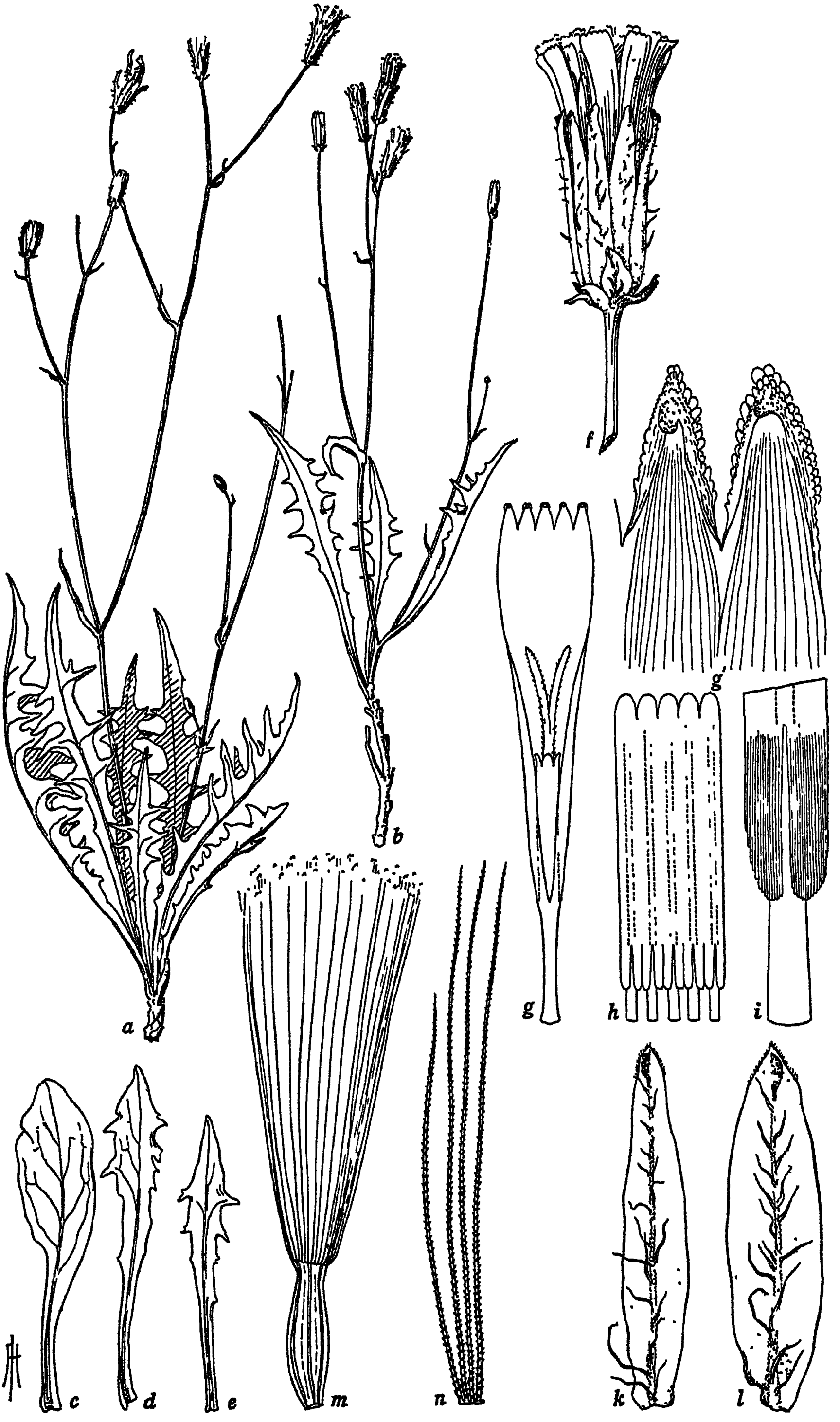

Fig. 4. *Youngia distincta*, from type: *a*, *b*, plant, × ½; *c*, *d*, *e*, caudical leaves, × 1; *f*, head, × 2; *g*, floret lacking ovary, × 4; *g'*, detail of ligule teeth, × 25; *h*, anther tube, × 8; *i*, detail of appendages, × 32; *k*, *l*, inner involucral bracts, × 4; *m*, immature achene and pappus, × 8; *n*, section through pappus showing 4 series of bristles, × 8.

Youngia distincta is closely related to *Y. serawschanica*. The following differences between the two have been noted by the present authors.

	Y. serawschanica	*Y. distincta*
Caudical leaves	Up to 7 × 2 cm.	Up to 11 × 2.5 cm.
Heads	4–6 flowered	About 9-flowered
Involucre	12–13 × 3 mm.	11–12 × 3–4 mm.
Involucre	Nearly glabrous	Strongly pubescent
Outer bracts	⅕–⅓ as long as inner	⅕–¼ as long as inner
Inner bracts	5–6 in number	8 in number
Anther-tube	6.25 mm. long	5 mm. long
Filaments	Extend 1 mm. beyond the anther tube	Extend 0.5 mm. beyond the anther tube
Pappus	2-seriate	4-seriate

In addition it was stated by the authors of *Y. distincta* that in this species the plant is larger and its stems more strongly angled; also that the flowers are a darker shade of reddish yellow. They express the opinion that *Y. distincta* cannot be considered as merely a form of *Y. serawschanica*. With this the present authors are inclined to agree. When mature achenes are available the evidence may be still more conclusive. The immature achenes of the two species are similar in general appearance and especially in the definite indication of unequal ribs. This last feature is one of the distinctive features of the genus *Youngia*. Both species show strong resemblance to *Youngia tenuifolia* in size and habit of the plant and size and shape of the leaves, the few-flowered heads, in both inner and outer involucral bracts, including the apical tubercles, and in floral characters. These two species may therefore be included in Sec. Crepidopsis (cf. Babcock and Stebbins. Carnegie Inst. Wash. Publ. No. 484:25, 46. 1937.)

II. THE GENUS AETHEORRHIZA

Some time ago (Babcock and Lesley, Univ. Calif. Publ. Agr. Sci. 2:325. 1926; Hollingshead and Babcock, *op. cit.* 6:28. 1930) the senior author pointed out that the chromosomes of the species generally passing as *Crepis bulbosa* (L.) Tausch are entirely different from those of any true species of *Crepis*. More recently, the junior author has studied the external morphological characteristics as well as the chromosomes of various genera in the Cichorieae, and from this study the true relationships of *C. bulbosa* have become evident. In its floral and fruiting characteristics as well as its chromosome complement, this species resembles the genera *Launaea* and *Sonchus* more nearly than *Crepis*. It is, however, sufficiently distinctive to warrant its recognition as a separate, monotypic genus. This was done long ago by Cassini, but a further description and discussion of his genus *Aetheorrhiza* seems advisable in the light of the newly discovered evidence.

Aetheorrhiza bulbosa (L.) Cass., Dict. Sci. Nat. 48: 425. 1827

(Figures 5, 6)

Perennial, 0.7–5.5 dm. high; root rhizomatous, stoloniferous, bearing leaves at the stolon-nodes, and with elongated fibers sometimes bearing a whitish subglobose tubercle 0.5–1.5 cm. in diameter; caudex slender, short or elongated, simple or branching, leafy; caudical leaves 1–25 cm. long, 0.4–3.5 cm. wide, spatulate, the blade elliptic, mostly acute, gradually attenuate in a long or short narrow petiole, entire, repand-denticulate, dentate or subpinnatifid, usually glabrous and ± glaucous, with pale or reddish midrib and petiole, rarely hispidulous: cauline leaves

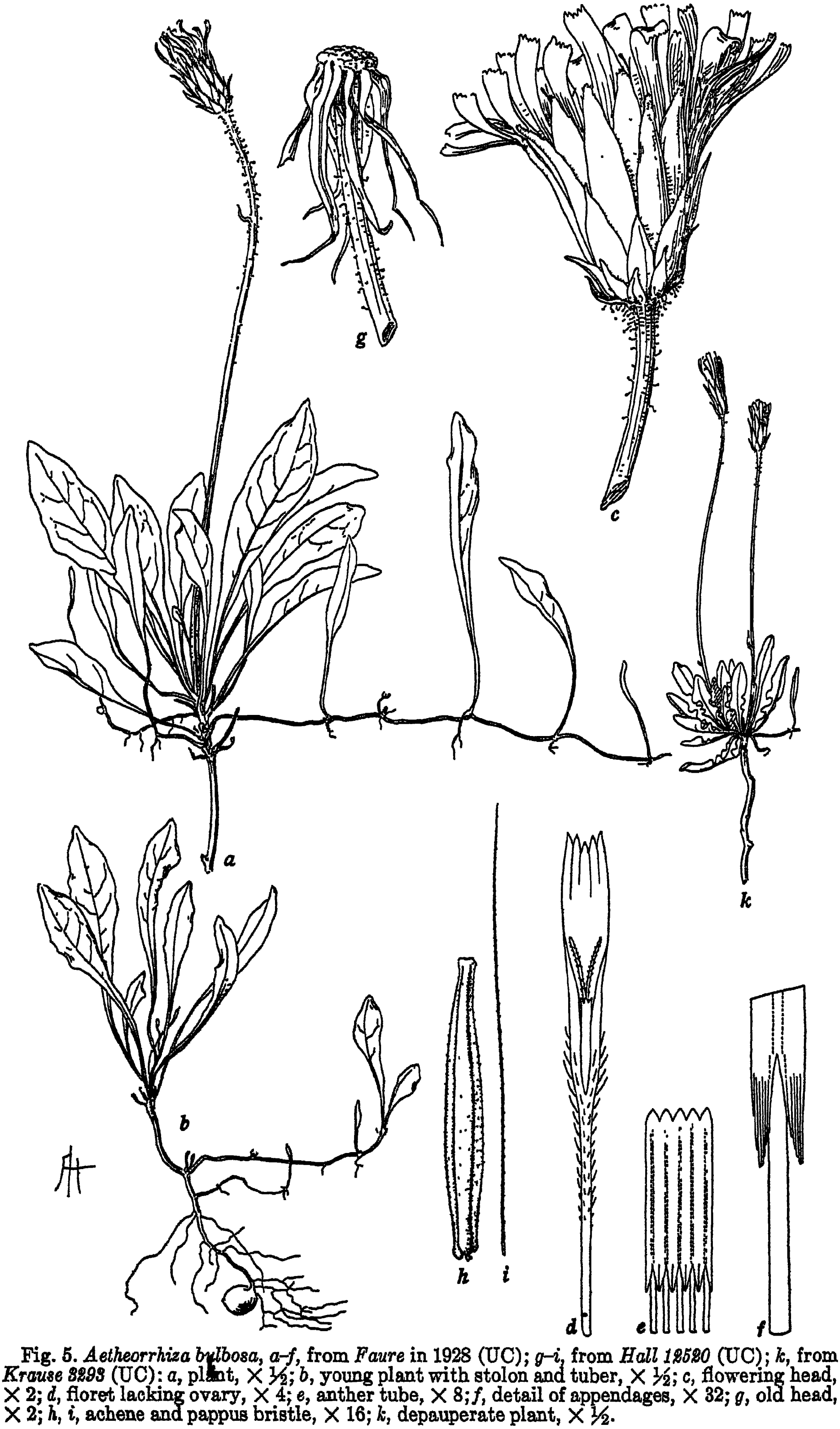

Fig. 5. *Aetheorrhiza bulbosa*, *a–f*, from *Faure* in 1928 (UC); *g–i*, from *Hall 12520* (UC); *k*, from *Krause 3293* (UC): *a*, plant, × ½; *b*, young plant with stolon and tuber, × ½; *c*, flowering head, × 2; *d*, floret lacking ovary, × 4; *e*, anther tube, × 8; *f*, detail of appendages, × 32; *g*, old head, × 2; *h*, *i*, achene and pappus bristle, × 16; *k*, depauperate plant, × ½.

absent except in occasional forms with one or two near the base resembling the caudical leaves or with one or more higher up and bractlike; stems scapiform, 1-headed, or rarely 1–3-furcate, 2–4-headed, terete, striate, glabrous below, usually pubescent above with blackish tack-shaped gland hairs; involucre cylindric-campanulate, 9–16 mm. long, 3–7 mm. wide at middle, the bracts mostly multiseriate, imbricate, sometimes the outer bracts fewer and much shorter than the inner ones, usually densely pubescent at the base with tack-shaped gland hairs, not thickened at maturity, ultimately reflexed; outermost bracts deltoid to lanceolate, often paler, the others lanceolate, acute, glabrous at apex and on inner face; receptacle areolate, areoles verrucose, glabrous; corolla 15–18 mm. long; ligule 1.75 mm. wide; teeth 0.4–0.8 mm. long; corolla tube 7–9 mm. long, densely pubescent above the middle with coarse acicular hairs up to 0.75 mm. long; anther tube about 3 × 1 mm. when opened out; appendages 0.5 mm. long, narrow, acuminate; filaments about 0.75 mm. longer; style-branches about 2 mm. long, 0.15 mm. wide, yellow or green; achenes pale brown, 3–5 mm. long, about 0.5 mm. wide, ± attenuate at the apex and swollen at the hollow base, fusiform, tetragonal with 4 deep narrow grooves from base to apex, the costae sometimes with a shallow groove on each side of the narrow median ridge; pappus white, 6–10 mm. long, copious, multiseriate, with broader and narrower setae intermixed, the setae ranging from about 15 to 80 μ wide, very finely barbellulate, strongly persistent. Flowering Feb.–June; flowers deep or pale yellow, the ligules with or without a reddish purple or sometimes a greenish stripe on the outer face; anther tube yellow; style-branches yellow or green. Chromosomes, $2n = 18$, small. (*Leontodon bulbosus* L., Sp. Pl. 798. 1853; *Hieracium bulbosum* Willd., Sp. Pl. 3: 1562. 1804; *H. tuberosum* Brot., Fl. Lusit. 1:318. 1804; *Apargia bulbosa* Balb., Mem. Acad. Tor. 1808:224; *H. stoloniferum* Viv., Fl. Ital. Frag. 17, t. 20. 1808; *Prenanthes bulbosa* DC., Fl. Fr. 4:7. 1815; *Crepis bulbosa* Tausch, Flora 11 (I Erg.):78. 1828; *Taraxacum bulbosum* Rchb., Fl. Exc. 270. 1830–32; *Aetheorrhiza montana* Willk., Oest. Bot. Zeitschr. 25:110. 1875; *Crepis bulbosa* var. *polycephala* Boiss., Fl. Or. 3:833. 1875; *C. montana* Marès, Cat. Bal. 176. 1880, non Urv., nec Tausch; *Crepis Willkommii* Burn. et Barb., Voy. Bot. 56. 1881; *Hieraciodes bulbosum* O. Kuntze, Gen. 1:345. 1891; *Crepis bulbosa* fa. *Willkommii* (Burn. et Barb.) Knoche, Fl. Bal. 2:517–523. 1922.)

The type of Linnaeus has not been seen by the present authors; but the following critical specimens have been examined: *Leontodon bulbosus* L., ex herb. Vaillant in Herb. Monspeliensis; *L. bulbosus* L., in Herb. DC., Prod. VII:160, n.1; *Hieracium bulbosum* Willd., *Aetheorrhiza bulbosa* Cass., *Prenanthes bulbosa* DC., and *Crepis bulbosa* Tausch, the last the type of Tausch, all in Herb. Bot. Inst. der deutschen Univ., Prag; *L. bulbosa*, *H. bulbosum* and *Apargia bulbosa*, in Herb. Willdenow, n. 14643–1, 2, 3. All of these specimens belong to the one species.

Distributed locally throughout the whole Mediterranean littoral and in adjacent uplands; western Europe in some maritime and adjacent localities as far north as the British Isles. It occurs in a wide variety of situations, such as the following: maritime sands, stationary dunes, gravelly or rocky shores, gravelly railway beds, shaded banks on sandy loam, a gorge in the interior of Crete among bushes, marshes in northern Tunisia, saline marshes in Cyprus, borders of fields and walls in Majorca and Portugal, also in dry calcareous gravel in montane Majorca from 700–1200 m. alt., on volcanic tuff in Sicily, in marshes on stiff, clay soil in Albania, and on dunes, in forest clearings and meadows, on sandy, silicious, and calcareous clays in Morocco.

Reduced forms frequently occur, especially in exposed locations near the sea. The wide variations in size of plant and parts of the plant, recorded in the foregoing description, correspond with the wide adaptability indicated by the remarkable range of environments noted by collectors. Except for these size differences, the ensemble or facies of the species remains fairly constant. Only two outstanding variants have been noted. One of these, represented by Knoche's plant from the mountains of Majorca (Ms) and Babcock's no. 319 (UC), is taller and more slender

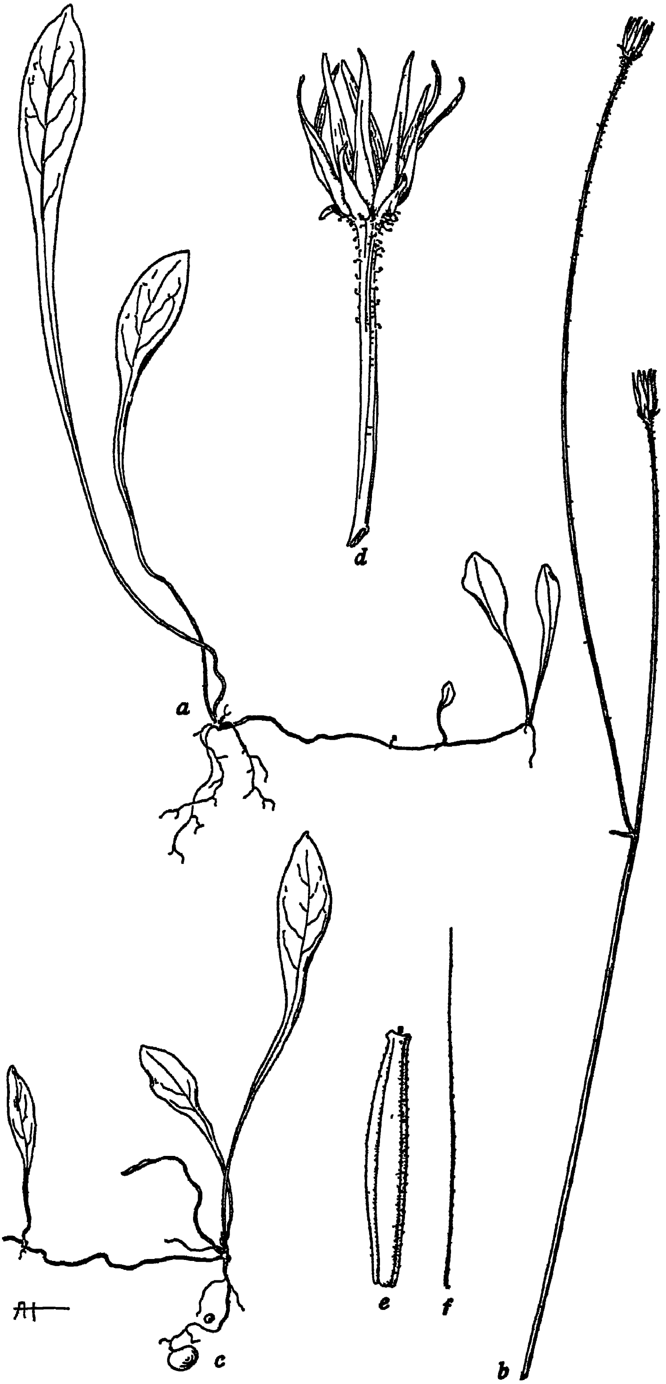

Fig. 6. *Aetheorrhiza bulbosa*, from *Babcock 319* (UC): *a–c*, plants and stem, × ½; *d*, mature head, × 2: *e*, *f*, achene and pappus bristle, × 8

than the usual form, with smaller involucres, and often with the stem 1–3-furcate, 2–4-headed. The specimens mentioned came from the interior uplands of Majorca and Crete. But according to Post (Fl. Syr. Pal. Sinai, ed. 2, 2:153. 1933) the longer stemmed, 2–4-headed variant named *A. bulbosa* var. *polycephala* by Boissier occurs on the coast as well as the interior of Palestine. The other peculiar variant (cf. *Pampanini 4560* (Fl)) has the leaves, stems, and involucres hispidulous with yellowish glandless setae and the characteristic tack-shaped gland hairs are entirely absent. This unique variation in pubescence is the more interesting because of the existence of typical plants in another locality (Wadi Saria) in the same district. This suggests that the wadis in the vicinity of Tarhuna may be effectively isolated from one another by the intervening more arid areas. The fact that the Tarhuna (Tarhona) escarpment is thought by geologists to represent the original coast line suggests that these local populations of *A. bulbosa* may be relics remaining from a once continuous and more variable population. More extensive collections in this region, followed by genetic studies, might throw considerable light on the relationships of *A. bulbosa* and other Cichorieaceous genera. It is possible that there exists considerable genetic variation in this species, affecting the plant's tolerance of marked chemical differences in the soil as well as differences in humidity, light, and temperature. It has been reported by one collector in Tripolitania that this plant is "a great favorite with all animals." It is stated by Bonnier and Douin (Fl. Illus. Fr. Suisse et Belg. 6:88. 1921–23) that the tubercles have been used against goitre.

Algeria: Oran, Batterie Espanole, *Faure* in 1928 (UC); Algiers, *Meyer* in 1879 (K). Tunisia: near Tabarca, *Eig* in 1930 (UC). Tripolitania: near Tripoli, swamps of Ain-Zara, *Miss Fenzi* in 1931 (UC); *ibid.*, *Pampanini 118* (Fl); Tarhuna, Wadi Saria, *Pampanini 1239* (Fl); Tarhuna, Wadi Msaaba, Kasr Doga, *Pampanini 4560* (Fl). Egypt: without locality, *Olivier and Bruguière* in 1794 (Ms). Palestine: near Haifa, Carmel, *Eig* in 1923 (UC, HU); between Kefar Uria and Hulda, *Eig* in 1922 (UC); Dschidro, *Smoly* in 1927 (HU). Syria: Beirut, *Barbey 571* (B). Turkey: Adana reg., Kurt Tepe, 153 m., *Balls 2096* (UC); Trojan region, Kenkoei, Dumbrek valley, *Ascherson 1131* (B); Prince's Islands, Prinkipo, *Krause 3293* (UC); near Istanbul, *Pichler* in 1874 (Bur). Greece: Crete, upper Samaria gorge, Neroutsiko spring, *Babcock 319* (UC); Thessaly, Volo region, Mt. Pelion, *de Heldreich and Holzmann* in 1883 (Bur); Zante, *Sibthorp 89* (O). Dalmatia: Ragusa, *Pichler* in 1872 (Bur). Italy: Istria, Pola, *Huter* in 1867 (Bur); Campania, Naples, Portici, *Pellanda* in 1912 (US, UC); Liguria, Bordighera, *Bicknell and Pollini* in 1914 (G); Abruzzi, Pescara, *Barbey* in 1873 (Bur); Elbe I., *Morrumi* (Bur); Sicily, Mt. S. Angelo above Cefalu, *Strobly* in 1874 (Bur); Trapani, *Ross 646* (Bur); Avola, *Rigo 85* (Bur). France: Corsica, near S. Lucia, *Briquet* in 1907 (Bur); Rousse I., dunes, *Briquet* in 1907 (Bur); Corsica, near Albo, *Briquet* in 1907 (Bur); Toulon, *J. Ball* in 1890 (US); Cap Brun, *Hall 12520* (UC); Île de Porquerolles, *Burnat et Cavillier* in 1906 (Bur); salins d'Hyeres, *Thiébaut* in 1877 (Bur); Var, Maurette, *Roguebrune* in 1898 (UC); Herault, Roque Haute, *Maillard* in 1857 (K); Aude, La Nouvelle, *Sennen* in 1901 (UC) Basses-Pyrénées, Pyrénées-Orient., Agly, *Guillon* in 1870 (K). Spain: Balearic Is., Majorca, Puig de Galatzio Mts., 300–1300 m., *Porta et Rigo* in 1885 (Bur); Pont d'Inca, *Bianor* in 1918 (Bur, UC); Majorca, *Knoche* (Ms); Malaga, Marbella, *Ceballos* in 1921 (UC). Portugal: near Lisbon, Alcantara valley, *Daveau* in 1877 (UC); Coimbra, Santa Clara, *Kostermans and Kruyt* in 1936 (G); Praia da Rocha, *Kostermans and Kruyt* in 1936 (G). England: Cornish coast, Anglesey, *Massey* in 1926 (K).

Aetheorrhiza bulbosa, in its floral characteristics, shows clear affinities to both *Launaea* and *Sonchus*. In particular, its achenes, with their four broad, rounded ribs, separated by narrow grooves, and their 4-notched bases, resemble closely those of many species of *Launaea*, such as *L. sarmentosa* (Willd.) Sch. Bip., (*L. pinnatifida* Cass.), which is either conspecific with or very closely related to the type species of the genus. The 4-ribbed, 4-notched condition reflects the ovary anatomy, which consists in many achenes of 4 vascular bundles, as in *Sonchus* and some species of *Launaea,* whereas in *Crepis* the ovary always contains 5 or more bundles. The achenes of *Aetheorrhiza* are, furthermore, somewhat obcompressed, and not terete, as in most species of *Crepis.* The corollas have the tubes nearly as long as the ligule, a feature which is typical of *Launaea* and *Sonchus,* but is seldom found in *Crepis.* The conspicuous white pubescence of the upper part of the corolla tube and base of the ligule also resembles that which is typical of *Launaea* and *Sonchus* but not of *Crepis.* The pappus in *Aetheorrhiza* also resembles that of *Launaea* and *Sonchus* in being a mixture of relatively broad and narrow setae, and in containing some setae which are united in pairs on their lower portion. Furthermore, the setae are more flexuous than those of most *Crepis,* with their barbs less conspicuous under the compound microscope. Both of these are characteristics of *Launaea,* in particular *L. sarmentosa,* a species with pappus setae all of the same sort. The involucres of *Aetheorrhiza* are more like those of *Sonchus* than of either *Launaea* or *Crepis.* They are broad and many-flowered, as in *Sonchus* and *Crepis,* while in *Launaea* they are usually narrow and few-flowered. Their numerous, more or less evenly imbricated bracts without scarious margins are similar to those of many species of *Sonchus,* but are found in only a few species of *Crepis* and in none of *Launaea.* Glandular pubescence at the base of the involucres and the apex of the peduncles is found in many species of *Sonchus* and *Crepis,* but not in *Launaea.* Furthermore, the peculiar tack-shaped gland hairs found in this species do not occur in *Crepis.* In habit, *Aetheorrhiza* differs considerably from *Sonchus, Launaea,* or *Crepis.* It is more nearly approached in this respect by *Launaea sarmentosa* than by any other species of these genera, since in both *L. sarmentosa* and *A. bulbosa* new rosettes of leaves are formed along elongated rhizomes. Moreover, in both of these species the peduncles are scapiform. In *Launaea,* however, as in *Sonchus,* the heads are never solitary on the peduncles as in *Aetheorrhiza.*

The somatic chromosome number, $2n = 18$, has been found in species of both *Sonchus* and *Launaea,* and the small size of the chromosomes is characteristic of the former genus.

To summarize, *Aetheorrhiza* resembles *Launaea* in its achenes, corollas, and pappus; *Sonchus* in its corollas, involucres, and its somatic chromosome complement; but it is unique in habit and has no obvious relationship to any particular species of either genus. Its recognition as a distinct genus which has diverged from a *Sonchus-Launaea* ancestral stock seems therefore fully justified.

CHROMOSOMES AND PHYLOGENY IN CREPIS

III. The Relationships of One Hundred and Thirteen Species

BY

E. B. BABCOCK AND J. A. JENKINS

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CONTENTS

PAGE
INTRODUCTION 241
METHODS AND MATERIALS 242
CHROMOSOME NUMBERS IN CREPIS 243
CREPIS KARYOTYPES 243
THE SECTIONS
Section 1. Desiphylion 244
Section 2. Spathoides 245
Section 3. Omalocline 245
Section 4. Brachypodes 247
Section 5. Mesomeris 247
Section 6. Soyeria 248
Section 7. Paleya 249
Section 8. Anisorhamphus 250
Section 9. Gephyroides 251
Section 10. Berinea 253
Section 11. Macropodes 254
Section 12. Ixeridopsis 254
Section 13. Intybellia 255
Section 14. Mesophylion 256
Section 19. Phaecasium 256
Section 20. Hostia 257
Section 21. Microcephalum 259
Section 22. Pterotheca 260
Section 23. Zacintha 260
Section 24. Phytodesia 261
Section 25. Lepidoseris 261
Section 26. Nemauchenes 263
Section 27. Psammoseris 266
DISCUSSION 267
Progressive Decrease in Chromosome Number 267
Increase in Asymmetry of the Chromosomes 269
Decrease in Chromosome Size 271
SUMMARY 273
TABLES 275
BIBLIOGRAPHY 289

CHROMOSOMES AND PHYLOGENY IN CREPIS

III. The Relationships of One Hundred and Thirteen Species

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INTRODUCTION

IN THE EXTENSIVE studies of the evolutionary processes in *Crepis* and related genera (Babcock and Lesley, 1926; Hollingshead and Babcock, 1930; Babcock and Cameron, 1934; Babcock, Stebbins, and Jenkins, 1937, 1942) two distinct categories of genetic change are evident: (1) gene mutations, which are responsible for the morphological and physiological diversity of the species, and which may also induce interspecific sterility; and (2) gross structural changes in the chromosomes (karyotype[1] changes), which are mainly important because of the genetic isolation they produce—isolation that leads to interspecific sterility. The evidence indicates that karyotype changes have proceeded independently of morphological changes in the plants, and that they have not directly contributed to morphological and physiological diversity. In many of the evolutionary lines of *Crepis* morphological change has been accompanied by changes in karyotype. However, in some groups of related species there have been marked morphological changes with little or no change in karyotype, and in still other groups there have been profound karyotype alterations associated with relatively slight morphological changes.

It has been pointed out (Babcock, Stebbins, and Jenkins, 1942) that there are distinct evolutionary trends in the karyotype diversity in *Crepis*, and that these karyotype changes may be summarized under the following classes:

(1) *A progressive decrease in the basic chromosome number* is the most outstanding karyotype change which has occurred in the genus *Crepis*. In spite of the fact that the majority of species have a basic number of four, the morphological and geographical evidence indicates that the primitive number is six, and those forms with three, four, and five as the haploid number, are definitely derived. There are a few exceptions to this progressive decrease in chromosome number and these involve either polyploidy or hybridization or both.

(2) *Polyploidy* is largely confined to the American species where, together with apomictic reproduction, it has resulted in a great diversity of forms, that is, in large species complexes. In the remainder of the genus doubling of the chromosome number has occurred on several occasions but on the whole has played a relatively minor role.

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[1] The term karyotype was first proposed by Delaunay (1922) as a systematic unit—the genus in its natural limits—which included those species with more or less similar chromosomes. Levitsky (1924) recognized the difficulty in applying such a definition since he demonstrated the incorrectness of Delaunay's idea of a revolutionary reorganization of nuclear elements in the formation of genera. Levitsky then proposed a new definition of karyotype, the sum of the characteristic physical properties of the chromosome complement: number, size, and structural peculiarities of the chromosomes of a set. Through usage by Letivsky and others it has come to mean the structures of the chromosomes visible at somatic metaphase. However, Dobzhansky (1941, p. 97) has extended the term to include details of structure that may not be visible but may be detected through alterations in pairing relations. In the present paper, the term is used to designate the visible structures of chromosomes, following Levitsky.

(3) *An increase in asymmetry* is manifested in two ways: (a) there is a tendency for the more advanced species to have karyotypes made up of chromosomes of unequal length and (b) the more advanced species have chromosomes with a more terminally situated centromere, which leads to a chromosome with one arm longer than the other.

(4) *A decrease in chromosome size* is the least well marked of the evolutionary trends, it is to a limited extent correlated with a parallel decrease in total size of plant but not invariably so. It is frequently associated with a specialized and restricted distribution of the species.

The present study is the culmination of twenty-five years of study in the genus *Crepis* and includes all of the species that are known cytologically, that is 113 out of the total of 196 in the genus. Chromosome counts and karyotype illustrations of the majority of the 113 species have been published in Parts I and II of this series (Hollingshead and Babcock, 1930; Babcock and Cameron, 1934). However, with additional material and further study, extensive taxonomic revision of the genus has been necessary. Changes in nomenclature of the previously published species together with new species reported for the first time are included in this paper.

MATERIAL AND METHODS

The karyotypes of the various species were studied exclusively from permanent preparations of root-tip metaphases obtained during the years 1921 to 1941 inclusive. All fixations were made from plants either grown from seed or from roots collected in the wild. Usually the root tips were taken from plants growing in four or six-inch pots; herbarium specimens and seed were usually taken from these same plants, thus insuring accurate identification and a permanent record.

At first, a chrom-acetic-formalin fixative (Hollingshead and Babcock, 1930) was followed by Heidenhain's iron-alum haematoxylin stain; however, several refinements were introduced, principally to shorten the time of preparation. Smith's (1934) crystal-violet schedule was substituted for the haematoxylin stain, and later Randolph's (1935) modification of the chrom-acetic-formalin mixture and schedule, followed by Stockwell's (1934) modification of Flemming's triple stain. Considerable study of the effects of these various methods on chromosome size and morphology indicate that they gave essentially similar karyotype images. If, in fact, there were differences due to the different fixatives and stains used they were so slight in comparison with other sources of variability as to be negligible.

A portion of the illustrations are identical with those used by Babcock and Cameron (1934) the remainder (drawings of those species marked with a star in table 1) are new. In the latter case, after a thorough study of slides of not less than three and usually more plants, the "best-spread" plate was selected, namely, one in which the chromosomes of a haploid set were shown in their true length (that is, lying in the horizontal plane). The haploid set was drawn by the aid of a camera lucida at a magnification of 5000 × and reduced one-half in reproduction. An essentially similar procedure was used by Babcock and Cameron (1934) with the exception that the original drawings were made at a magnification of 3750 × and reduced to two-thirds their original size in reproduction. Thus both sets of illustrations are at the same magnification, 2500 ×.

CHROMOSOME NUMBERS IN CREPIS

A detailed taxonomic study of the genus *Crepis*, carried on by the senior author, has necessitated numerous changes in nomenclature within the genus (Babcock, 1941); in addition, some species previously reported as *Crepis* have been referred to other genera. In order to avoid confusion the chromosome numbers of all *Crepis* species previously reported by members of this laboratory are summarized in table 1. In all, some two thousand accessions of *Crepis* species have been examined cytologically, but only those new accessions are listed in table 1 that provide new information—species reported for the first time are starred. The species that have been transferred to other genera are listed in table 2.

CREPIS KARYOTYPES

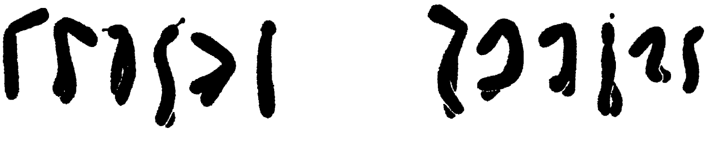
THE SECTIONS

The sections in *Crepis* were set up primarily on the basis of morphological similarities and discontinuities with the aid of evidence from geographical distribution. Karyotype similarity was used in a few cases in deciding to which of two closely related sections a particular species belonged; that is, karyotype evidence was used only to a very limited extent in giving weights to the morphological discontinuities between the sections. This restricted use of karyotype evidence in delimiting the sections thus has very little effect in accentuating or obscuring the evolutionary trends in karyotype changes.

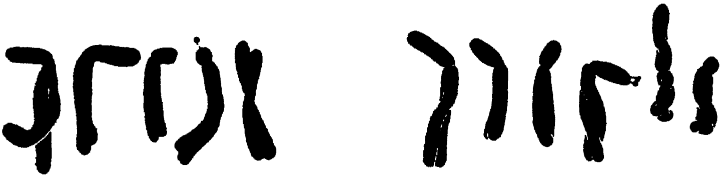
The sections are numbered in order of their evolutionary advancement, so far as this can be accomplished by a linear series. In the illustrations, a similar attempt was made to arrange the species within each section and subsection in order of their evolutionary advancement—the more primitive species being towards the bottom or on the left in horizontal arrangements.

The morphological criteria of relative degrees of primitiveness or advancement of the species are based on the work of Small (1919) who reviewed the phyletic concepts of earlier specialists on the Compositae and proposed a phylogenetic scheme for the whole family. Although some of Small's general conclusions on phyletic criteria do not hold for *Crepis*, the following characterizations are in general agreement with his concepts. The more primitive species are those possessing several or all such features as: a perennial root and suffrutescent or woody caudex; the root rhizomatous or, if deeply penetrating, very strong and woody; large, lyrate-pinnatifid or nearly entire leaves; tall, robust stems or, in alpine species, scapiform stems; few, large flowerheads; the involucre poorly differentiated into outer and inner series of bracts or with very large outer bracts, and the inner bracts remaining unchanged at maturity; large florets; large, fusiform or coarsely beaked achenes; and coarse, stiff pappus bristles. The most advanced species are small, very precocious annuals; with small, often dissected leaves and low, slender stems bearing many small heads; the involucre with very few small outer bracts and the inner bracts specialized by cortical thickening; very small florets; very small achenes with a fine, delicate beak; and very fine, soft pappus bristles.

Between these two extremes there exist groups (sections) of species exhibiting various degrees of advancement or specialization. Within many such groups there is a considerable range from more primitive to more advanced species. The most general evolutionary trend in morphology within the genus is reduction—reduction in length of life cycle, accompanied by reduction in size and durability of the root; reduction in size of the plant, except in the case of the low, scapose, alpine species which are primitive; and reduction in size of the leaves, heads, florets, and fruits. Furthermore, in several of the sections some of the species are characterized by their own peculiar marks of specialization. For example, in the more primitive sections the achenes are homogeneous or uniform in shape; but in six of the more advanced sections they are of two or even three distinct types. Although in many sections it is difficult, because of unlike variability in different parts of the plant, to arrange the species in a linear phyletic series; and although similar difficulties arise even in arranging the sections in a linear series; yet it is believed that the order presented in the following arrangement is a fairly close approximation to the true, natural relationships of the groups.



C. viscidula 3178 C. paludosa 1825



C. sibirica 1862 C. geracioides 3456

Fig. 1. Species of Section 1, Desiphylion.

Section 1. Desiphylion

In this most primitive section of *Crepis*, the only exception to the haploid number six is *C. sibirica* ($n = 5$), which is the most primitive species in the genus. While there are some morphologically similar chromosomes, in each of the species the main picture is one of distinct karyotypes; for example, the satellited chromosomes are different in each species. All of the species, with the exception of *C. paludosa*, the most advanced in the section, contain a pair of large median[2] chromosomes, and, in general the arm ratio of the *paludosa* chromosomes is somewhat greater than in the other species. The morphological diversity of these species is paralleled by karyotype diversity.

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[2] For the sake of brevity, the *Crepis* chromosomes will be referred to as: median, submedian or subterminal, when the arm ratio (=length long arm/length short arm) is: 1.0, up to 2.0, or greater than 2.0, respectively. Knob chromosomes are those subterminal chromosomes in which the short arm is spherical in shape.

SECTION 2. SPATHOIDES

This section contains the single species *C. kashmirica*. Except for the nearly entire instead of lyrate leaves, this species might be classified in section 1. It is generally similar to the species of section 1, and in size of its involucres and achenes it is less reduced than *C. viscidula* and *C. paludosa* of section 1. Although the haploid number is six, the karyotype is different from any species of section 1. The average arm ratio is the smallest in the genus: the chromosomes are the most symmetrical. Even the satellited chromosome is submedian, in which it resembles *C. geracioides*, one of the two most primitive species in the genus. If it is assumed that the ancestral karyotype was made up of equal-sized, median chromosomes, *C. kashmirica* has varied less in chromosome symmetry than any other species of *Crepis*. The combined evidence from comparative morphology and karyology indicates that *C. kashmirica* is one of the most primitive species in the genus.

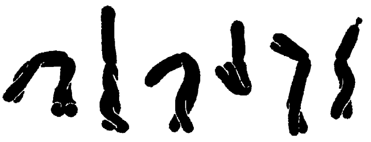


Fig. 2. Species of Section 2, Spathoides

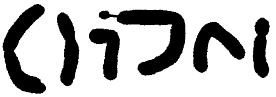


Fig. 3. Species of Section 3, Omalocline.

SECTION 3. OMALOCLINE

The karyotype of *C. pygmaea*, the only species of this section, has the haploid number six, like the previous sections, with the exception of *C. sibirica*. It does not differ markedly from them in arm ratio of the individual chromosomes, but none of the *pygmaea* chromosomes has its exact counterpart in any previously discussed species. In addition, it is distinctive in the smaller total length of chromosomes, and in the greater diversity in length of the individual chromosomes—one of them being definitely smaller than any chromosomes in the two previous sections. Morphologically *C. pygmaea* suggests definite relationship with sections 1, 4, and 5, and even with species of the related genera *Soroseris*, *Youngia*, and *Dubyaea*. It is certainly a primitive species.

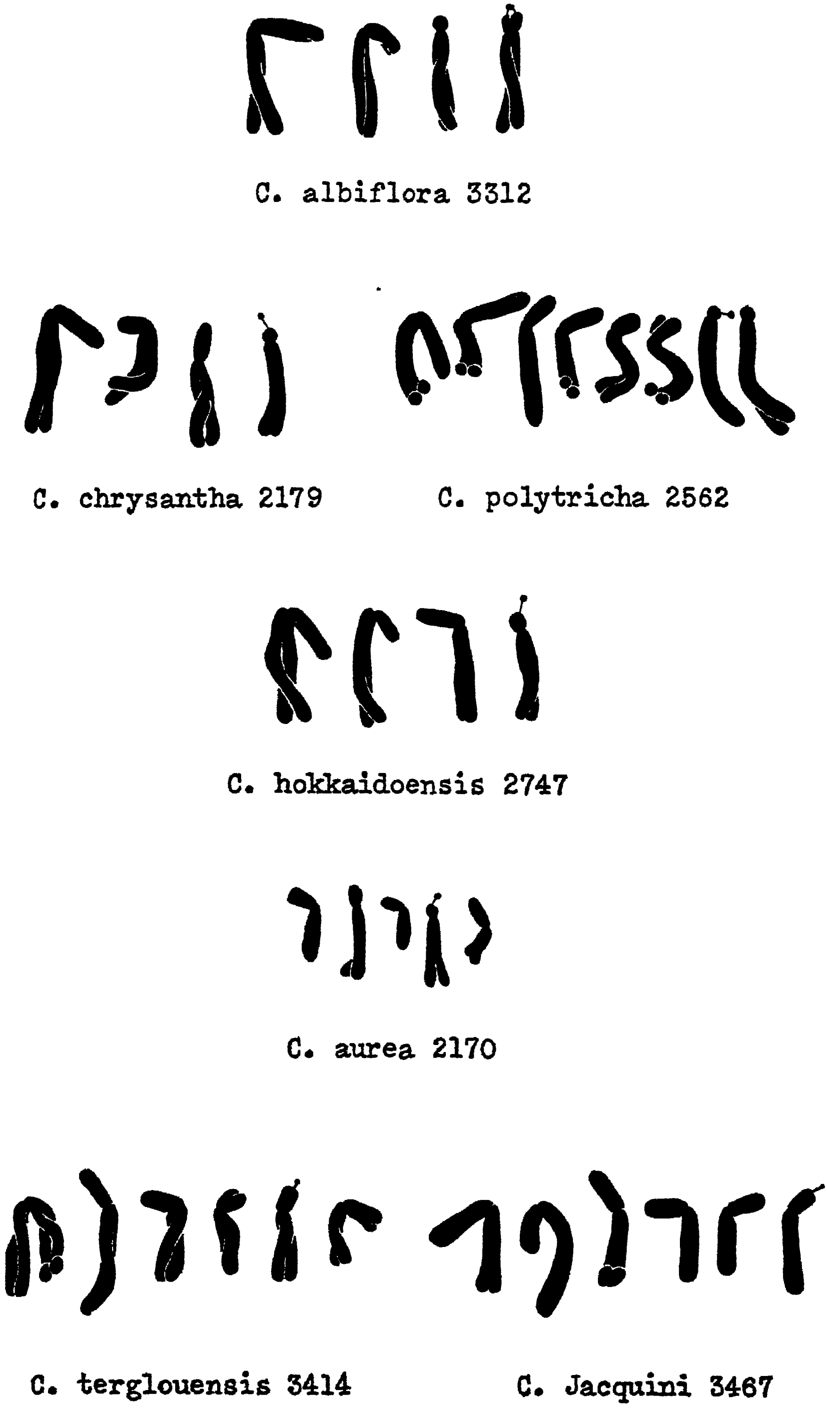


Fig. 4. Species of Section 4, Brachypodes.

SECTION 4. BRACHYPODES

The eight species of Brachypodes, all but one of which is known cytologically, are a very diverse group karyologically, although morphologically, they have well-marked common characteristics, especially the praemorse or short, rhizomatous root and the scapiform stems. All are found in high montane locations but in different regions, and have rather restricted distributions. The two most primitive species, *C. terglouensis* ($n = 6$) and *C. Jacquini* ($n = 6$) both from the European Alps, have some karyotypical resemblances, but in common with the other six-paired species in the first three sections, each has a distinct karyotype.

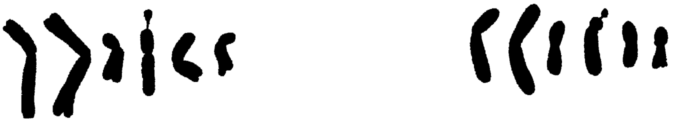
Morphologically, *C. Jacquini* ($n = 6$), *C. aurea* ($n = 5$), *C. chrysantha* ($n = 4$), and *C. polytricha* ($n = 8$) form a fairly distinct subgroup in an ascending phylogenetic series within the section. As is clear from figure 4, they are karyotypically quite diverse, not only in number but also in symmetry: the chromosomes within the species show considerable size inequality, and considerable variability in arm ratio. Furthermore, the total chromosome length in *C. aurea* is definitely shorter than in the others, which is parallel with the reduction in plant size. In this series *C. polytricha* and *C. chrysantha* have the most nearly similar basic karyotypes, and the former undoubtedly represents doubling of one or more species closely related to *C. chrysantha* karyologically. In this group of species the morphological evidence certainly indicates that the changes in haploid chromosome number followed the sequence six, five, four, eight in their evolutionary development.

C. hokkaidoensis ($n = 4$) and *C. albiflora* ($n = 4$) are morphologically more distinct from the other two groups and from each other, and their chromosomes have somewhat different arm ratios.

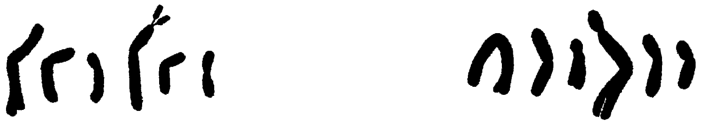
SECTION 5. MESOMERIS

The seven species of this section, which have been investigated cytologically, comprise a well-marked group on the basis of such common characters as the rhizomatous root, more or less branched stem, medium-sized heads, and beakless achenes. But on the basis of habit, degree of reduction in size, and presence or absence of brown wool at the base of the leaves, they fall into two groups. The first, *C. lapsanoides* ($n = 6$), *C. lyrata* ($n = 6$), and *C. mollis* ($n = 6$), show some morphological resemblance to *C. viscidula* ($n = 6$) of section 1. While there are some differences in the arm ratios of the individual chromosomes of the three species, there is a very striking general similarity in the karyotypes, which parallels their close morphological resemblance. The karyotypes show no marked resemblance to that of *C. viscidula* and, in general, the chromosomes are somewhat thinner than in the latter species.

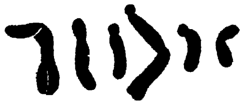
The second group, *C. willemetioides*, *C. hierosolymitana*, *C. montana*, and *C. Mungierii*, also with six pairs of chromosomes, are not so similar karyotypically as the first group. In all four species there is some reduction in total chromosome length as contrasted with the first group. This karyotype reduction is paralleled by reduction in plant size, and the parallel is most marked in the case of *C. Mungierii;* however, the arrangement of the species in order of reduced size of plant is not the same as that on the basis of decreasing chromosome length.



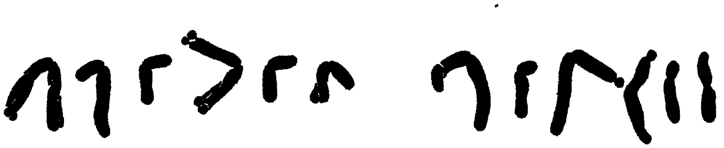
C. montana 1175 C. Mungierii 2877



C. willemetioides 3217 C. hierosolymitana 2619



C. mollis 2201

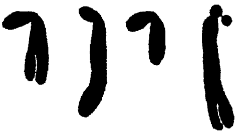


C. lapsanoides 3466 C. lyrata 1644

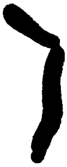
Fig. 5. Species of Section 5, Mesomeris.

SECTION 6. SOYERIA

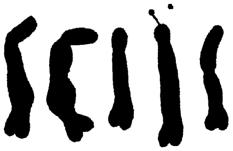
Three of the four species in this section are known cytologically. *C. pontana* ($n = 5$) is closely related to *C. sibirica* ($n = 5$) of section 1, and except for the deep-rooted habit and the non-lyrate leaves could pass as a member of section 1. The karyotypes of these two species are also very similar—there is only a slight difference in the arm ratios of the two karyotypes. *C. conyzaefolia* ($n = 4$) is rather close morphologically to *C. pontana* and the two species do not differ significantly in total chromosome length. It seems that this is the second case (cf. sec. 4) where the reduction from the five- to the four-paired condition occurred. *C. blattarioides* ($n = 4$), on the other



C. blattarioides 2033

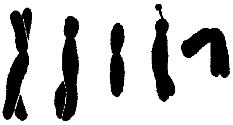


C. conyzaefolia 2183



C. pontana 2204

Fig. 6. Species of Section 6, Soyeria.



C. albida 2088

Fig. 7. Species of Section 7, Paleya.

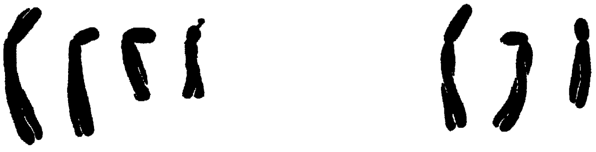
hand, has a marked chromosome inequality and a smaller total length of chromosomes, and morphologically is not so closely related to the other two species of this section as they are to each other. In its very unusual karyotype, it resembles that of *C. alpestris* of section 8—this similarity will be discussed later.

SECTION 7. PALEYA

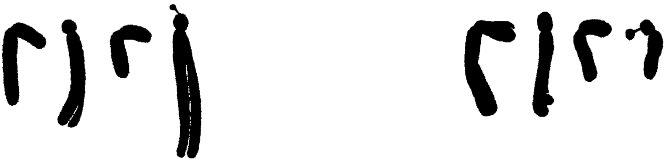
C. albida ($n = 5$) is the only one of the three species in this section that is known cytologically. In comparison with the other three five-paired species discussed up to this point, the karyotype resembles that of *C. aurea* of section 4, but it is reduced in total chromosome length, and it is much more asymmetrical than the karyotypes of *C. sibirica* (sec. 1) and *C. pontana* (sec. 6), which resemble one another. *C. albida* exhibits definite morphological similarities to species in sections 20 and 25, which will be discussed later.

SECTION 8. ANISORHAMPHUS

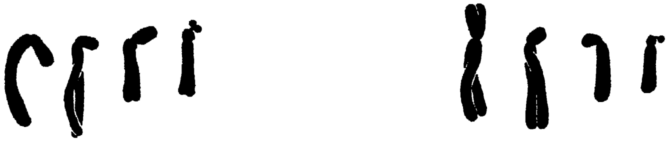
Of the twenty-six species in this section, nearly all of which are indigenous to central and southern Africa, only six, all with four pairs of chromosomes, have been studied cytologically. Morphologically these six species are divided into two groups of three: *C. kilimandscharica*, *C. alpestris*, and *C. suffruticosa* are in the first, or more primitive group, and *C. hypochaeridea*, *C. Newii*, and *C. scaposa* are in the second. Unlike the previous sections, the karyotypes of all these species, with the single exception of *C. alpestris*, are remarkably similar; there are only very slight variations in size and in arm ratio of some of the chromosomes. These five species show rather wide morphological diversity with practically no change in karyotype, indicating that morphological and karyotype changes may proceed independently. *C. alpestris*, as mentioned above, has a very unusual karyotype which is similar to that of *C. blattarioides* of section 6. In fact, these two species hybridize where they come to-



C. Newii 3274   C. scaposa 3301



C. alpestris 2512   C. hypochaeridea 3399



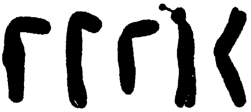
C. kilimandscharica 3280   C. suffruticosa 3281

Fig. 8. Species of Section 8, Anisorhamphus.

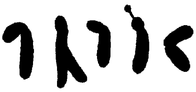
gether in the Alps; though, as judged by garden hybrids, the F_1 plants are completely sterile. Morphologically, however, *alpestris* exhibits much more resemblance to some of the primitive African species than to *blattarioides*.

SECTION 9. GEPHYROIDES

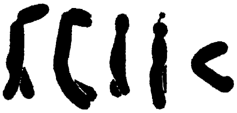
All three species in this section have a haploid chromosome number of five, and there are certain common morphological features, such as the low, slender stems, glabrous foliage, and similar involucres, flowers, and fruits. There is, however, considerable morphological diversity within the section, and the species show relationships to several other sections, indicating that it might be considered as a connecting link between several sections. While all of the species have five pairs of chromosomes, the karyotypes of two of them, *C. tingitana* and *C. leontodontoides*, have more resemblances to species of other sections than they have with each other. *C. tingitana*, the most primitive of the three, has a karyotype which resembles that of *C. pontana* of section 6, except for the proportionately somewhat smaller size of all chromosomes, and like *C. pontana* its karyotype is not very different from that of *C. sibirica*. The karyotype of *C. leontodontoides* is very similar to that of *C. aurea* of section 4, except



C. suberostris 2829

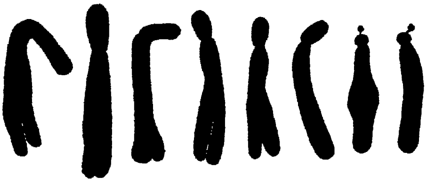


C. leontodontoides 1807

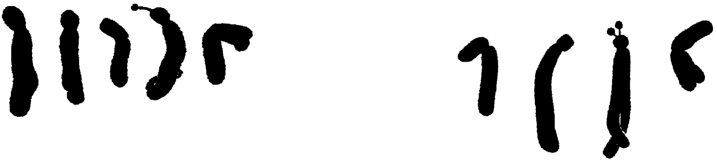


C. tingitana 1681

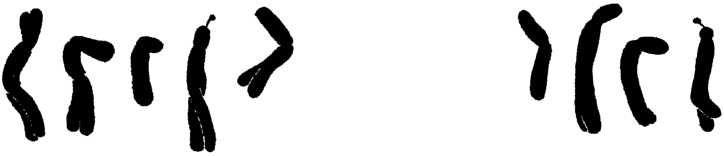
Fig. 9. Species of Section 9, Gephyroides.



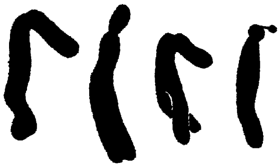
C. incana 1667



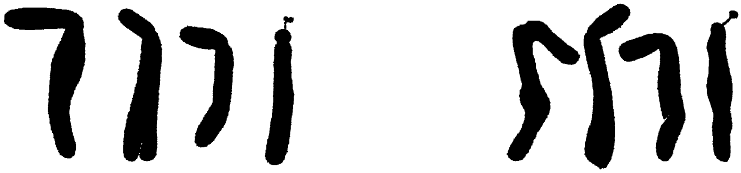
C. Raulinii 2875 C. oporinoides 3398



C. Baldaccii 3417 C. Triasii 2945



C. chondrilloides 1907



C. pannonica 1695 C. latialis 1914

Fig. 10. Species of Section 10, Berinea.

that all of the *leontodontoides* chromosomes are proportionately somewhat smaller, and in addition the long arm of the *leontodontoides* satellited chromosome is smaller still. Since the hybrid between these two species usually has five pairs of chromosomes (Avery, 1930), the karyotype resemblance is more than superficial. The karyotype of *C. suberostris*, the only annual species so far discussed, resembles somewhat that of *C. tingitana*, but there are several points of difference (see fig. 9).

SECTION 10. BERINEA

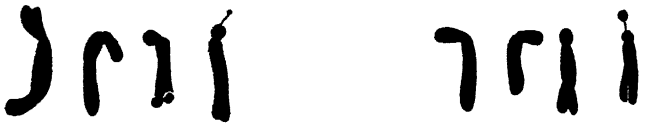
Of the twenty-nine species in this section only eleven have been investigated cytologically. Three of the latter, *C. biennis* ($n = 20$), *C. ciliata* ($n = 20$) and *C. taygetica* ($n = 20$), are polyploids, and since their basic chromosome sets have not, as yet, been definitely established, they are not illustrated in figure 10.

On the basis of size and habit of plant the species of this section have been grouped into four subsections, only the first three of which are represented by the species reported here. In addition to the octoploids, *C. biennis* and *C. ciliata*, the first subsection contains the closely related species *C. pannonica* ($n = 4$), *C. latialis* ($n = 4$), and *C. chondrilloides* ($n = 4$). Parallel with their close morphological relationship is an obvious similarity of karyotypes, which resemble that of *C. conyzaefolia* (sec. 6). The second subsection contains five species, only two of which are known cytologically. *C. Baldaccii* ($n = 5$) and *C. Triasii* ($n = 4$). *C. Baldaccii*, the most primitive of the cytologically investigated species in the subsection, has a karyotype resembling that of *C. pontana* (sec. 6). *C. Triasii* is much more advanced morphologically than *C. Baldaccii* and its karyotype bears considerable resemblance to that of *C. blattarioides* (sec. 6). In the third subsection four species, *C. Raulini* ($n = 5$), *C. oporinoides* ($n = 4$), *C. incana* ($n = 8$), and *C. taygetica* ($n = 20$), out of a total of nine are known cytologically. At present it is unknown whether the polyploid *C. taygetica* has a basic set of four or five. The other polyploid *C. incana* has a basic set of four chromosomes, which resembles that of *C. pannonica*. *C. Raulini*, the most primitive species in this subsection, has a karyotype which bears no close resemblance to that of any other five-paired species. The karyotype of *C. oporinoides*, on the other hand, is very similar to the karyotypes of the four-paired *blattarioides* (sec. 6) and *C. alpestris* (sec. 8).

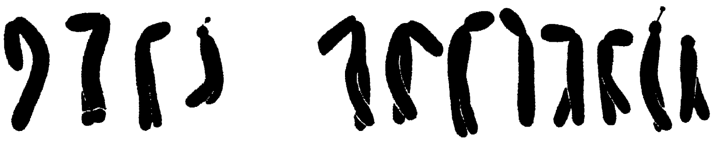
It is unfortunate that the four most primitive species in subsection 1 have not been studied cytologically. It is probable, however, that they are five-paired species and that their karyotypes would resemble those of *C. Baldaccii* of the second subsection and *C. pontana* of section 6. This prediction is based on morphological resemblance and on the fact that the polyploid species in the first subsection, *C. biennis* and *C. ciliata*, have been shown to be octoploids on a basis of five (Collins, Hollingshead, and Avery, 1929; Babcock and Swezy, 1935). In subsections 2 and 3 the most primitive single species are *C. auriculaefolia* and *C. Raulini* respectively. Both of these species occur on the high mountains of Crete. It would be interesting to compare their karyotypes, but the former has not been studied cytologically. On morphological grounds *C. auriculaefolia* would be expected to be five-paired, with the chromosomes more like those of *C. Baldaccii* than *C. Raulini*. The two four-paired species representing subsections 2 and 3, *C. Triasii* and *C. oporinoides*, differ from each other not only in habit but in numerous morphological details; though each shows more morphological resemblance to the primitive member of its own

Section 11. Macropodes

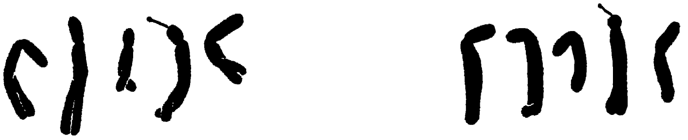
Six of the fourteen species in this section have been examined cytologically, and these six species belong in four morphological groups: (1) *C. Schachtii* ($n = 5$) and *C. bithynica* ($n = 5$); (2) *C. oreades* ($n = 4$) and *C. crocea* ($n = 8$); (3) *C. Hookeriana* ($n = 4$); (4) *C. Robertioides* ($n = 4$). The karyotypes of the two most primitive species, *C. Schachtii* and *C. bithynica,* are very similar except for the small subterminal pair. The karyotype of *C. oreades* does not resemble closely any of the previous four-paired karyotypes, and similarly *C. Hookeriana* has a distinct karyotype. The karyotype of *C. Robertioides* is not very different from that of *C. Hookeriana.* Here again morphological diversity is paralleled by karyotype diversity. As pointed out by Babcock and Cameron (1934), the karyotype evidence is consistent with the hypothesis that *C. crocea* is an amphidiploid hybrid between *C. oreades* of this section and *C. Bungei* of section 14.



C. Hookeriana 1458   C. Robertioides 3129



C. oreades 2981   C. crocea 2352



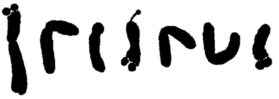
C. Schachtii 3240   C. bithynica 3218

Fig. 11. Species of Section 11, Macropodes.

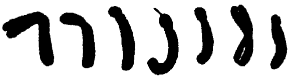
Section 12. Ixeridopsis

Only three of the seven species in this section have been examined cytologically and all three have seven pairs of chromosomes, which is an unusual number in the genus. There is some difference between the three species, *C. flexuosa, C. nana,* and

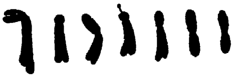
C. elegans, in the relative size of the chromosomes and in the arm ratios of the individual chromosomes, but they are much more alike in karyotype than they are like any other *Crepis* species. In morphology, they are also well separated from the other *Crepis* species, and, as the name of the section suggests, show many resemblances to the related genus *Ixeris*, in which the haploid number seven is also found. It has been suggested (Babcock, Stebbins, and Jenkins, 1937) that section Ixeridopsis may have originated through intergeneric hybridization at an early stage in the development of the two genera, both of which are assumed to have developed from the same ancestral group of species of the genus *Dubyaea*. These ancestral species, which probably had seven pairs of chromosomes, are apparently now extinct.



C. elegans 2654



C. nana 2698



C. flexuosa 2983

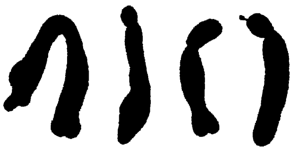
Fig. 12. Species of Section 12, Ixeridopsis.

SECTION 13. INTYBELLIA

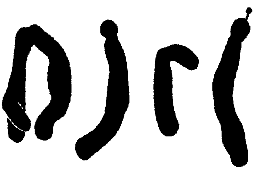
The three species in this section, *C. gymnopus*, *C. praemorsa*, and *C. incarnata*, all have praemorse roots, which indicates a phylogenetic connection with sections 1–5, all of which are characterized by the rhizomatous type of root. The karyotypes of all three are remarkably similar and quite distinct from any of the four-paired karyotypes so far discussed. This is another section within which there has been considerable morphological diversity without any accompanying karyotype change—that is, morphological and karyotype evolution have proceeded independently.

SECTION 14. MESOPHYLION

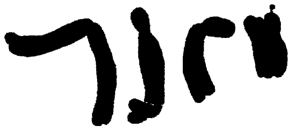
The three species in this section, like those in section 9, may be considered as transitional, since they show definite relationship to the primitive section 4, and, at the same time, have a number of advanced morphological characters. The karyotypes of the two species known, *C. Bungei* ($n = 4$) and *C. tectorum* ($n = 4$), are very similar and show a remarkable resemblance to those of *C. chrysantha* and *C. hokkaidoensis* of section 4. Thus, here again, there has been considerable morphological change with little, if any, change in karyotype.



C. incarnata 1304



C. praemorsa 2133

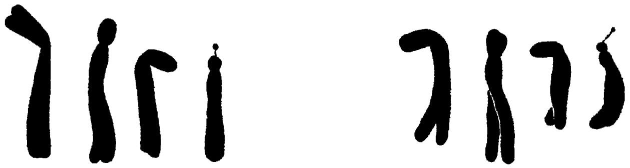


C. gymnopus 2746

Fig. 13. Species of Section 13, Intybellia.

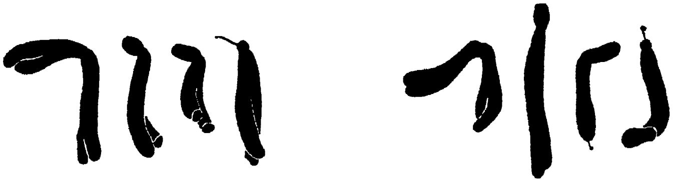
SECTION 19. PHAECASIUM

The species in this section would be included in section 13 except for the deep tap root. In fact, *C. Reuteriana*, the most primitive species in the section, has a woody, somewhat elongated root stock, which bears many strong secondary fibers, indicating that the deep-rooted habit is a derived character. Five out of a total of six species have been examined cytologically and all have essentially similar karyotypes; karyotypes which are also similar to those in section 13. This fundamental similarity of karyotypes again emphasizes the point that morphological and karyotypical evolution are independent processes.

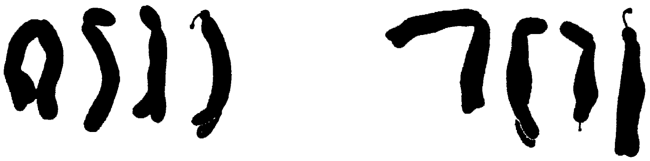


C. Bungei 1827 C. tectorum 1498

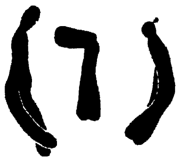
Fig. 14. Species of Section 14, Mesophylion.



C. Stojanovii 3176 C. pterothecoides 3232



C. palaestina 1552 C. pulchra 1483



C. Reuteriana 2218

Fig. 15. Species of Section 19, Phaecasium.

SECTION 20. HOSTIA

Of the nine species in this section, seven have been investigated cytologically. These seven species can be divided into four rather well-defined morphological groups: (1) *C. alpina* ($n = 5$), *C. syriaca* ($n = 5$);[3] (2) *C. rubra* ($n = 5$); (3) *C. foetida*

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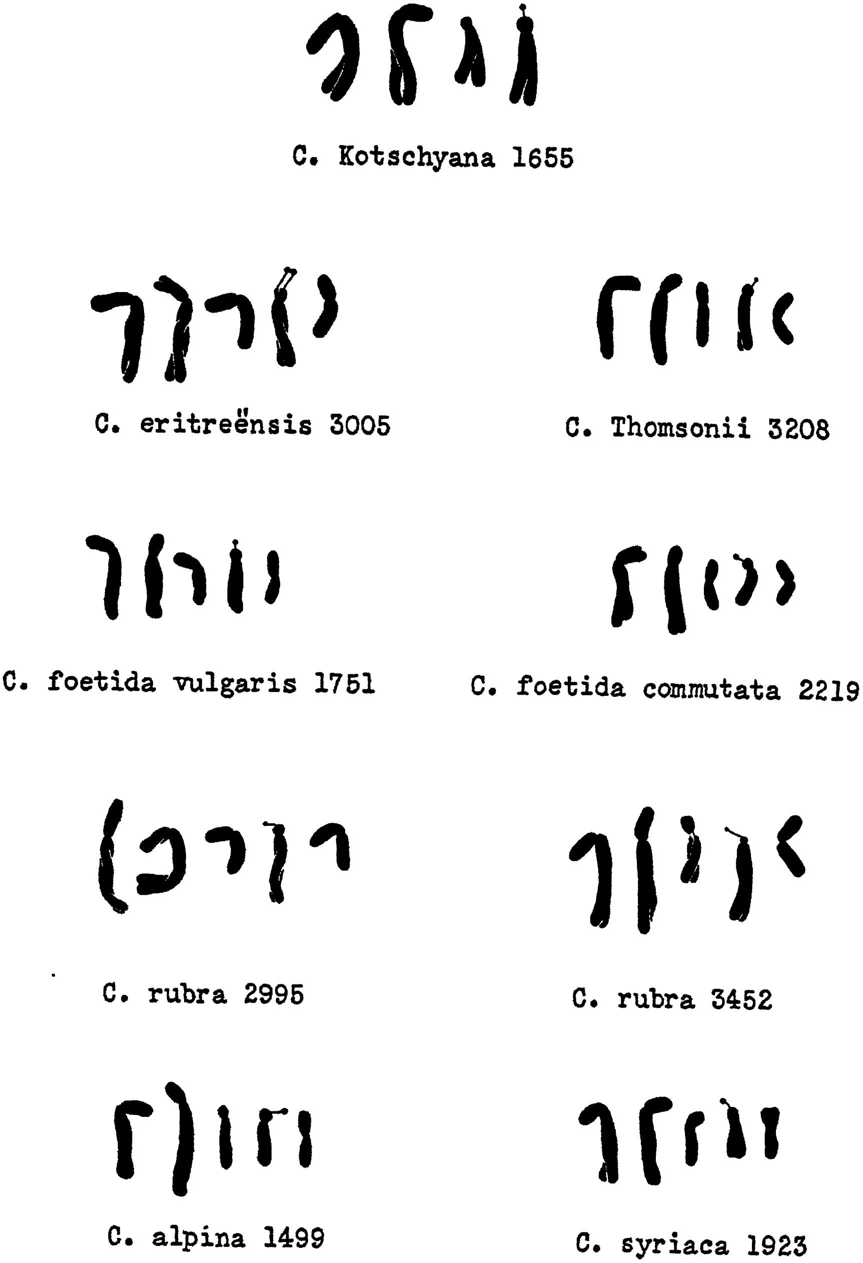
[3] The basic number in *C. syriaca* is 5; however, *C. syriaca* plants frequently have extra chromosomes—the somatic numbers 10–18 inclusive have been observed by Cameron (1934).



C. Kotschyana 1655

C. eritreënsis 3005

C. Thomsonii 3208

C. foetida vulgaris 1751

C. foetida commutata 2219

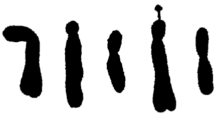
C. rubra 2995

C. rubra 3452

C. alpina 1499

C. syriaca 1923

Fig. 16. Species of Section 20, Hostia.



C. multicaulis 1480

($n = 5$), *C. eritreënsis* ($n = 5$), and *C. Thomsonii* ($n = 5$); (4) *C. Kotschyana* ($n = 4$). The two most primitive species, *C. syriaca* and *C. alpina*, have very similar karyotypes, which resemble that of *C. albida* of section 7 to which they are closely related.

C. rubra is not only distinct morphologically from *C. alpina* and *C. syriaca* but it is also distinct karyotypically. Hollingshead and Babcock (1930) illustrated two different strains of *C. rubra* (1506 and 1176), both of which possessed one pair of short chromosomes with a large satellite, but differed in that one (1176) had, in addition, another pair of chromosomes with very small satellites. Koller (1935) reported a strain of *C. rubra* from Edinburgh that had no satellites.

A careful reëxamination of strains 1506 and 1176 together with three new strains (2888, 2995, and 3452) showed that in some metaphase plates of all five strains both the large and small satellites were clearly evident. However, the satellite threads were frequently contracted to such an extent that the satellites were drawn into the body of the chromosome—the homologous members of a pair behaved similarly in regard to the contraction. Numerous plates were found in which the small satellited pair appeared as an almost medianly constricted pair of chromosomes very similar to the other pair of small median chromosomes. Numerous other plates were found in which the small satellites on the larger pair of chromosomes were not visible. Some cells were found in which no satellites were evident, but none of the five strains showed a consistent lack of satellites as reported by Koller (1935) in the Edinburgh strain.

The main difference between the strains of *C. rubra* is in the frequency of cells showing contracted and extended satellite threads. In 1506 the large satellites were usually present, but the small satellites were only rarely seen; in 2888, 2995, and 3452 the large satellites appeared as integral parts of the chromosomes and the small satellites were usually evident, and in 1176 both pairs of satellites were usually visible. Further variability was found in the short arm of the chromosome which carried the small satellite; it was spherical in shape, usually with a diameter equal to that of the long arm; however, it was sometimes smaller, particularly in strain 3452, where it was often less than half its usual diameter. This is the second case of karyotype polymorphism within this section.

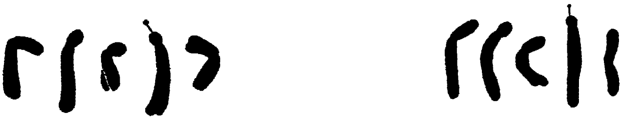
In the third group *C. foetida* and *C. Thomsonii* have very similar karyotypes while that of *C. eritreënsis* is different from them and from any other karyotype in the section. Here, again, is a case where morphological relationship and karyotypical similarity are not parallel. Hybrids between *C. Kotschyana*, the only four-paired species in this section (Sherman, unpublished), indicate that the karyotype of *C. Kotschyana* was derived from one of the five-paired species, or from one of their immediate ancestors through a series of chromosome interchanges. Thus, in the section as a whole, morphological change has been accompanied by considerable karyotypic change.

SECTION 21. MICROCEPHALUM

Only one out of a total of four species in this section is known cytologically. Although *C. multicaulis* ($n = 5$) has many advanced characteristics, most notably its extreme reduction in size of parts, yet its praemorse fibrous roots indicate relationship with the more primitive sections, characterized by rhizomatous roots. Its karyotype is remarkably similar to those of *C. aurea* (sec. 4), *C. albida* (sec. 7) and *C. leontodon-*

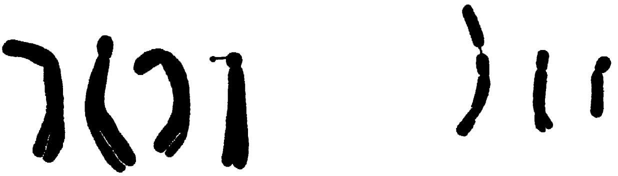
SECTION 22. PTEROTHECA

C. sancta ($n = 5$), the only species in this section, has no very close morphological relationships to any of the previous sections, but karyotypically it is very similar to *C. multicaulis* (sec. 21), and thus also to *C. aurea* (sec. 4), *C. albida* (sec. 7) and *C. leontodontoides* (sec. 9). Morphologically it shows more resemblance to *C. multicaulis* than to any of the other species mentioned.

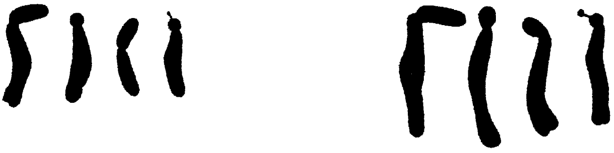


C. sancta nemausensis 3160 C. sancta bifida 3087

Fig. 18. Species of Section 22, Pterotheca.



C. multifolra 3062 C. Zacintha 3439



C. patula 2839 C. Dioscoridis 1455

Fig. 19. Species of Section 23, Zacintha.

SECTION 23. ZACINTHA

Morphologically the four species in this section may be divided into three groups; (1) the primitive *C. patula* ($n = 4$); (2) the intermediate *C. Dioscoridis* ($n = 4$) and *C. multiflora* ($n = 4$); (3) the advanced *C. Zacintha* ($n = 3$). Each group is characterized by a single distinctive karyotype. While *C. patula* is the most primitive species in the section it is specialized and reduced in some characters, and in comparison with *C. Dioscoridis* and *C. multiflora* of the second group the chromosomes are distinctly smaller, being both somewhat thinner and shorter in total length.

Thus, *C. patula* is an exception to the progressive decrease in chromosome size with evolutionary advancement. However, in view of its specialization in some characters and reduced plant size the exception is more apparent than real. The karyotypes of *C. Dioscoridis* and *C. multiflora* are very similar and distinctive. Finally *C. Zacintha*, the most advanced species in the section, has both a smaller number and size of chromosomes.

SECTION 24. PHYTODESIA

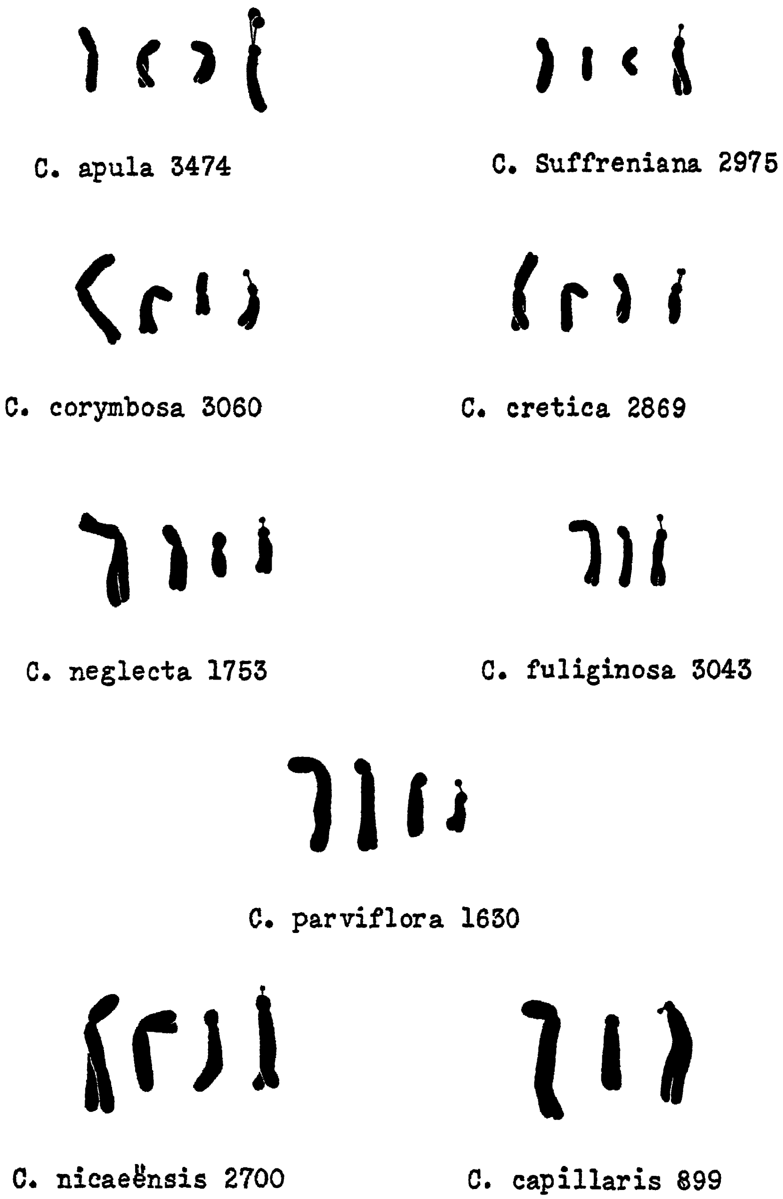
Of the ten species in this section, all but one have been investigated cytologically, *C. nicaeënsis* ($n = 4$), the most primitive species in the section, bears a very close morphological resemblance to the polyploid species *C. biennis* ($n = 20$) of section 10. Since the basic number in *biennis* is five, the two species may be assumed to have had a common five-paired ancestor; and the derivation of *C. nicaeënsis* was accompanied by reduction in chromosome number. Progressive reduction in chromosome number has proceeded still further within the section. *C. capillaris* ($n = 3$), though definitely related to *C. nicaeënsis*, is a more advanced species. *C. parviflora* ($n = 4$) shows many resemblances to *C. capillaris*, but it has a karyotype distinct from the other two species. In the remaining six species, which are morphologically much reduced and specialized in comparison with the above three, there has been a marked decrease in total size of chromosomes.

C. neglecta ($n = 4$), *C. fuliginosa* ($n = 3$), *C. corymbosa* ($n = 4$), and *C. cretica* ($n = 4$) form a very closely related morphological group—some taxonomists have even considered them to be forms of the same species; yet their karyotypes are very different in chromosome number, size, and individuality. This again emphasizes the point that morphological and karyotype evolution may proceed independently. Extensive studies on the hybrids of *C. neglecta* × *C. fuliginosa* (Tobgy, 1943) indicate that these two species possess the same genes arranged in different pairing blocks. Thus, some of their karyotype differences are due to chromosome rearrangements.

Both *C. apula* ($n = 4$) and *C. Suffreniana* ($n = 4$) are closely related to the *neglecta* complex, but each has a distinctive karyotype. *C. Suffreniana* shows a further decrease in total chromosome size, which is correlated with a decrease in plant size.

SECTION 25. LEPIDOSERIS

Nine of the thirteen species in this section have been studied cytologically and all have essentially the same four-chromosome karyotype. Some of the subspecies of *C. vesicaria* have tetraploid forms. In addition, some of the species, for example, *C. Fontiana*, *C. Bourgeauii*, and *C. lybica* seem to have chromosomes which are slightly larger. However, a large number of hybrids between the species of this section have been examined (Jenkins, 1939 and unpublished), and in no case was there any observable difference between the parental mitotic chromosomes; furthermore, meiosis was regular throughout with no unpaired segments at pachytene. Thus, it may be assumed that these species have the same arrangement of genes throughout. The great morphological diversity in the section demonstrates again that morphological change is not necessarily associated with karyotypic change. The sterility barriers between the species of this section are not due to chromosome incompatibilities but rather are gene determined.



C. apula 3474

C. Suffreniana 2975

C. corymbosa 3060

C. cretica 2869

C. neglecta 1753

C. fuliginosa 3043

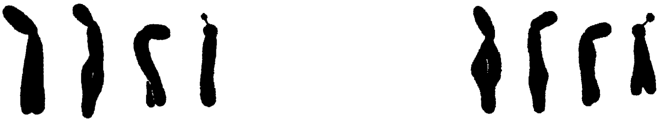
C. parviflora 1630

C. nicaeënsis 2700

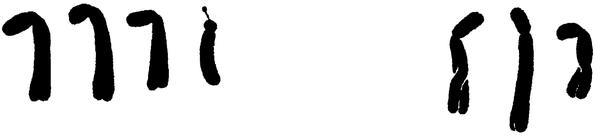
C. capillaris 899

Fig. 20. Species of Section 24, Phytodesia.

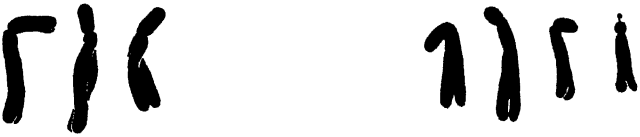
The karyotype of this section resembles very closely that of most of the species of section 8, though there are some slight differences in arm ratio of the individual chromosomes. There is little close morphological resemblance between Lepidoseris species and those of section 8. But one species of section 25, which has not been examined cytologically, does show considerable resemblance to species of section 8;



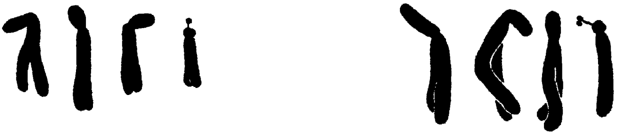
C. lybrica 1698 C. Marschallii 1532



C. divaricata 2980 C. Noronhaea 3022



C. Bourgeauii 3475 C. canariensis 3049



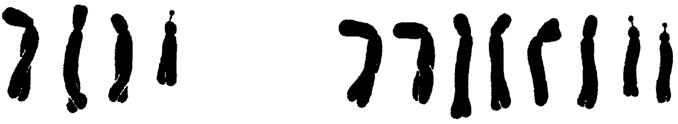
C. Clausonis 2848 C. Fontiana 3225

Fig. 21. Species of Section 25, Lepidoseris.

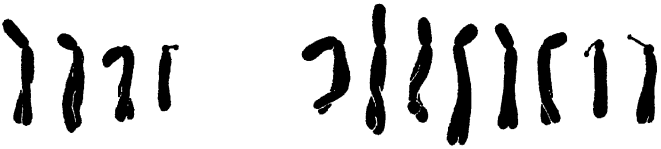
and its location in the Saharan Atlas is consistent with the idea that it may represent a connecting link between the two sections. It should also be noted that there is marked resemblance between some forms of the polymorphic *C. vesicaria* of section 25 and *C. achyrophoroides*, an Abyssinian species of section 7, which has not been examined cytologically.

SECTION 26. NEMAUCHENES

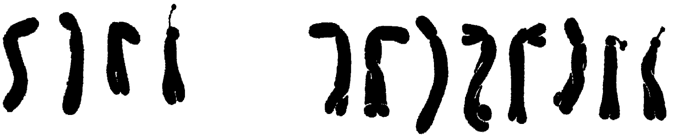
Of the seven species in this section, five have been studied cytologically; all five have four pairs of chromosomes. Morphologically *C. juvenalis* and *C. aculeata* are the most primitive, and *C. aspera* and *C. setosa* the most advanced, with *C. amplexifolia* more



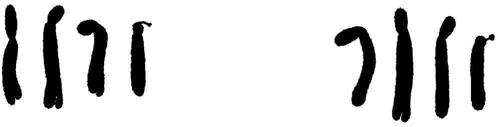
C. vesicaria myriocephala 2840 C. vesicaria myriocephala 2844



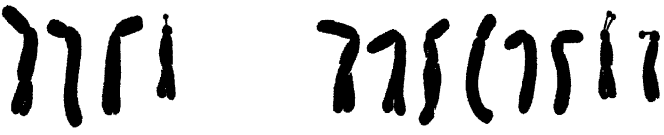
C. vesicaria stellata 2847 C. vesicaria stellata 3473



C. vesicaria taraxacifolia 1064 C. vesicaria taraxacifolia 1873

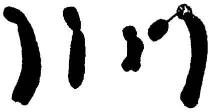


C. vesicaria andryaloides 2817 C. vesicaria hyemalis 3053

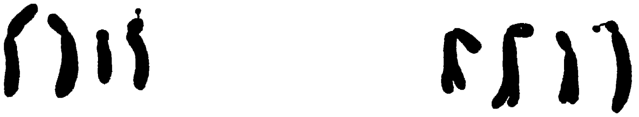


C. vesicaria typica 3236 C. vesicaria typica 2948

Fig. 22. Species of Section 25, Lepidoseris.

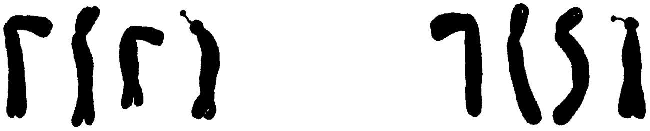


C. setosa 1036



C. amplexifolia 1019

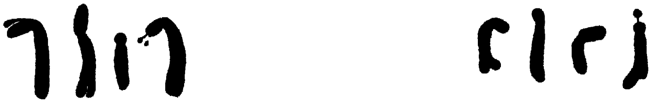
C. aspera 1135



C. juvenalis 3205

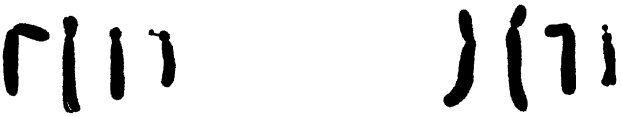
C. aculeata 1602

Fig. 23. Species of Section 26, Nemauchenes.



C. nigricans 3020

C. senecioides 2061



C. bellidifolia 2921

C. bursifolia 1220

Fig. 24. Species of Section 27, Psammoseris.

or less intermediate. *C. juvenalis* and *C. aculeata* have rather similar karyotypes, though the third chromosome from the left in the latter (fig. 23) is considerably longer. Furthermore the karyotype of *C. juvenalis* is very similar to those of the species of section 25, a similarity which is paralleled by some morphological resemblances.

C. amplexifolia, *C. aspera*, and *C. setosa* have significantly smaller chromosomes than the two species last mentioned. This reduction in karyotype size is not paralleled by reduction in plant size, but is paralleled by a reduction in flower and fruit size. Each of these three species has a distinct karyotype, but those of *C. aspera* and *C. setosa* are much more alike and differ only in having the third chromosome from the left in *C. setosa* (fig. 23) shorter than the corresponding chromosome in *C. aspera.* This difference in length is compensated for by the larger satellite in *C. setosa.*

SECTION 27. PSAMMOSERIS

The four species that have been investigated in this section have four pairs of chromosomes. In *C. bellidifolia* and *C. bursifolia* the plant is perennial, whereas *C. nigricans* and *C. senecioides* are short-lived annuals. On this basis the first two may be considered as more primitive. On morphological grounds, especially the degree of reduction in size of heads, flowers, and fruits and in specialization of the achenes, *C. senecioides* is certainly the most advanced species in the section and in the genus as a whole. The reduction in chromosome size, which was noted in the most advanced species of section 26, is even more marked in *C. senecioides.* Although there are many similar chromosomes as well as general similarity in the karyotypes of these four species, yet each is distinct, and there is no basis for arranging the four species in subgroups with respect to their karyotypes.

DISCUSSION

PROGRESSIVE DECREASE IN CHROMOSOME NUMBER

When the sections are arranged in a linear series, from primitive to advanced (table 3), it is obvious that there has been a general decrease in haploid chromosome number from six to three. The six-paired species are entirely confined to the first five, or most primitive sections. None of the last five sections contains any five-paired species. Though the four-paired species are the most numerous and occur in most sections, they make up a greater proportion of the most advanced sections and do not occur at all in the three most primitive sections. The three-paired species are confined to two of the most advanced sections. In addition to this main trend from six to three there are a few exceptional numbers.

The haploid chromosome number seven is found in section 12, Ixeridopsis, and in the related genus *Ixeris*. This, together with the morphological resemblances of these two groups, led to the assumption (p. 255) that the haploid number seven arose as a result of intergeneric hybridization when *Ixeris* and *Crepis* were in a formative stage. Three eight-paired species are obvious polyploids on the basis of four; an hypothesis which is consistent with both cytological and morphological evidence. The three twenty-paired species are also polyploids; *C. biennis* and *C. ciliata* are octoploids on the basis of five (cf. p. 252) and *C. taygetica* is either an octoploid on the basis of five or a decaploid on the basis of four. The remaining species with exceptional numbers are all American polyploids, which form a related polyploid series on the basis of eleven. The morphological and distributional evidence strongly supports the hypothesis that the original eleven-chromosome species arose as the result of several hybridizations between four- and seven-paired or possibly six- and five-paired species (Babcock and Stebbins, 1938, p. 27).

Rosenberg (1918) assumed that three was the most primitive number in *Crepis*, and that the higher numbers were derived as a consequence of duplication of single chromosomes or whole sets. Marchal (1920) considered four as the primitive number, largely because most of the species he counted were four-paired. He believed that *C. capillaris*, the only three-paired species then known, was derived from a four-paired ancestor by fusion of two chromosomes. Hollingshead and Babcock (1930) came to the conclusion that the five-paired species were morphologically more primitive than four-paired species, in spite of the fact that the latter are much the more numerous. They also concluded that the three-paired species are of more recent origin. Quite apart from the contradictory morphological evidence, Hollingshead and Babcock (1930) pointed out that Rosenberg's hypothesis was not supported by experimental work: it was early demonstrated that hyperploid plants were weak and soon reverted to the original number, so that it was very unlikely, on theoretical grounds, that the origin of aneuploid *Crepis* numbers could have arisen in such a manner. Marchal's hypothesis had the added difficulty of deriving a stable chromosome from a fused chromosome with two spindle fibers.

Babcock and Cameron (1934) presented new evidence to show that there had been a progressive decrease in chromosome number, and assumed that reciprocal translocation was the most likely process by which the decrease could occur. Since 1934 the study of several additional primitive species showed that they had six pairs of chromosomes, and thus firmly established the evolutionary decrease from six to three. A study of karyotypes in related genera has indicated that the most primitive numbers in the subtribe Crepidinae are eight and nine (Babcock, Stebbins, and Jenkins, 1937), thus a phylogenetic decrease in the chromosome number must have taken place in *Crepis* ancestors, a tendency which has continued within the genus itself.

Navashin (1932) proposed a scheme based on Belling's discovery of translocations, by which it was possible both to increase and decrease the chromosome number by a series of simple translocations and fragmentations without involving the *de novo* origin of a centromere. The central point of this "dislocation hypothesis" is that the increase or decrease in chromosome number could occur without losing any essential chromatin, thus making it possible to obtain fully viable new types. Furthermore, the hypothesis provided a mechanism for the production of morphologically new chromosomes. Experimental proof of Navashin's dislocation hypothesis was provided by Dubinin (1934, 1936) who obtained lines of *Drosophila melanogaster* through a series of reciprocal translocations, both with increased and decreased chromosome number. Also utilizing reciprocal translocations, Gerassimova (1939) produced *Crepis nova* I and II. In these four-paired *Crepis tectorum* derivatives there was no change in plant morphology or chormosome number, but there were profound alterations in chromosome morphology. Furthermore, when *C. nova* I was crossed with normal *C. tectorum*, the hybrids were only 30 per cent fertile, a decrease in fertility as great as that found in many interspecific hybrids.

The process of repeated reciprocal translocation will result in both increase and decrease of chromosome number, though a decrease will be expected somewhat more frequently. Increase in chromosome number involves two rare events in sequence: the addition of an extra centromere to the set by non-disjunction with consequent gene unbalance, and the transfer to it of some vital material before it is lost. On the other hand, the decrease in chromosome number does not involve this initial gene unbalance. The production of a "naked centromere," in which all of the vital material has been transferred to other chromosomes, does not disturb the gene balance, and the process may proceed at a very slow rate. It is even possible that there is some selective advantage in the low chromosome number itself. Mather (1941) has suggested that linkage of genes, in acting as a deterrent to free recombination of multiple genes, permits the majority of individuals of a population to have the optimum combination of multiple genes without eliminating the reserve of variability, which may be called upon when environmental conditions change. By decreasing the number of linkage groups there is less opportunity for the occurrence of extreme deviates and the consequent elimination of the genes determining them. These genes may be of great value to the plant under changed environmental conditions. That is, linkage will tend to suppress extreme variants without decreasing the potential variability; the fewer the number of linkage groups, the greater will be the suppression of these extreme variants.

Cytological analysis of closely related *Crepis* species with different chromosome numbers lends additional support to Navashin's hypothesis that increase or decrease in chromosome number may be achieved through translocations. In the case of *C. neglecta* ($n = 4$) and *C. fuliginosa* ($n = 3$) of section 24, morphological and distributional evidence strongly indicate that *C. fuliginosa* was derived from *C. neglecta* or an immediate ancestor of it. Study of hybrids between these two species (Tobgy,

1943) demonstrates the essential correctness of Navashin's hypothesis. The fact that very few unpaired regions were observed at pachytene in the F_1 hybrid shows that both species have essentially the same chromatin content. Meiotic analysis showed that a little more than half of the small median chromosome of *neglecta*, including the spindle attachment, was not present in *C. fuliginosa*. Staining reactions indicated that the missing portion was heterochromatic. Fundamentally the karyotypes of these two species are merely different arrangements of the same material, in spite of the fact that the total metaphase length of *C. fuliginosa* chromosomes is decidedly less than that of *C. neglecta*, quite apart from the missing portion of the small median chromosome. The karyotype differences between these two species are mainly due to two reciprocal translocations plus a general decrease in the metaphase length of *fuliginosa* chromosomes. However, in addition there were several other rearrangements: small translocations and inversions.

In section 20, Hostia, all the species have five pairs of chromosomes except *C. Kotschyana*. Morphological and distributional evidence indicates that this species was derived either from one of its closest relatives, *C. alpina*, *C. syriaca*, *C. rubra*, *C. foetida*, *C. eritreënsis*, or *C. Thomsonii*, or from some common ancestral species. Cytological analysis of the hybrids between *Kotschyana* and its five-paired relatives (Sherman, unpublished) again showed that the differences in karyotypes were due to a series of reciprocal translocations. As in the *neglecta-fuliginosa* case more rearrangements, translocations and inversions, had occurred than would be suspected from a visual comparison of the karyotypes.

Thus, all the evidence is consistent with the hypothesis that the main trend in chromosome number in *Crepis* has been a progressive decrease from a basic number of six to one of three and that this decrease took place in steps—the loss of one chromosome at a time. Each step in decrease occurred independently on several different occasions. In addition to the main trend of decrease in chromosome number there have been special groups in which an increase has occurred due to hybridization followed by amphidiploidy, sporadic cases of both auto- and allopolyploidy in the European species and extensive polyploidy in the western American species.

INCREASE IN ASYMMETRY OF THE CHROMOSOMES

On the basis of extensive observations in the subfamily Helleboreae, Levitsky (1931) advanced the hypothesis that a karyotype made up of equal-sized, equal-armed chromosomes is to be regarded as primitive, and asymmetry either in the size of chromosomes within the set or in the position of the centromere of the individual chromosomes represents a derived condition. Levitsky recognized two processes leading to asymmetry: (1) a progressive shortening through successive fragmentations of one or both arms of the chromosome; (2) a rearrangement due to translocations. Though Levitsky seems to favor the first process, which was also postulated by Delaunay (1926), it is difficult to subscribe to the idea of evolution by loss.

In the process of decreasing chromosome numbers by unequal reciprocal translocations it follows logically that there will be considerable alteration in symmetry, both in regard to the size of the chromosomes and the position of the centromeres. Unequal reciprocal translocations and inversions across the centromere—the latter may be regarded as reciprocal translocations of the chromosome ends—are the most important structural changes in karyotype evolution. Since large duplications and deletions (fragmentations) produce gene unbalance in basic species, it is doubtful that they have been involved in karyotype changes. Small duplications and deletions, on the other hand, have occurred in *Crepis:* Tobgy (1943) showed that some *C. neglecta* chromatin, probably heterochromatic, was not present in *C. fuliginosa,* the derived species; Collins (1924) found several cases of duplicate genes in *C. capillaris.* However, as far as we are able to judge at present, small duplications and deficiencies have not played a major role in karyotype changes. Inversions within a chromosome arm and equal translocations have also occurred in *Crepis* (Müntzing, 1934; Tobgy, 1943; Sherman, unpublished). Although they have a profound effect on pairing relations in hybrids, thus acting as isolating mechanisms, they have no visible effect on the karyotype. Hence the karyotype changes in *Crepis* leading to asymmetry in the chromosomes can be largely traced to the occurrence of unequal reciprocal translocations.

A series of reciprocal translocations results in two opposing tendencies: a tendency to preserve the symmetry of the chromosomes, and a tendency to make them more unequally armed. Starting from a symmetrical karyotype a series of unequal reciprocal translocations will inevitably produce an asymmetrical karyotype. Such a result was obtained by Levan (1935) in *Allium* because of the action of X rays. If it is assumed that breaks occur at random throughout the total length of chromatin, the longer arms will be involved more frequently in reciprocal translocations than the shorter arms. Furthermore the longer arms will more frequently act as donors, that is, will lose longer segments than they receive (Lewitsky and Sizova, 1934; Navashin and Gerassimova, 1935). Thus there will be a definite tendency for the karyotype to return to the symmetrical condition. In spite of this tendency toward symmetry, however, there is ample opportunity for the origin of very asymmetric chromosomes due to the fact that very short arms will not be involved in translocations very frequently. Further, there is also opportunity for the origin of chromosomes with two very short arms, which may, if they are largely composed of heterochromatic material, be instrumental in increasing or decreasing the chromosome number (Dubinin, 1936).

Do breaks occur at random throughout the total length of chromatin? This question assumes considerable importance in regard to the total number of new karyotypes that are likely to occur. If definite points are more liable to break ("weak points") the same karyotype may arise repeatedly. However, if breaks are distributed at random throughout the length of the chromosome it is very unlikely that the same karyotype will arise on several occasions, even with a very large number of translocations. Thus, if breaks are distributed at random similar karyotypes indicate that the species have a close phylogenetic relationship. The evidence on this question is somewhat fragmentary, and has the further difficulty that it has been obtained either from X ray induced rearrangements or those induced through aging seed. The fact that in *Crepis capillaris* Levitsky and Sizova (1934) with X rays and Navashin and Gerassimova (1935) with aged seed obtained essentially the same results, strengthens the hypothesis that induced and spontaneous translocations are comparable. In both cases, if it is assumed that all translocations are reciprocal, the frequency of chromosome breakage is roughly proportional to their total length. Essentially the same conclusion was obtained by Anderson (1935) in corn, and by Bauer, Demerec, and Kaufman (1938) in *Drosophila,* though in the latter case there was some indication of "weak points." More recent studies on *Drosophila,* Glass (1940), Helfer (1941), and Hinton (1942) give further evidence for the existence of the non-random distribution of breaks, but the deviation from random is not large. Giles (1940) showed that there were a preponderance of spontaneous breaks in the immediate region of the centromere in *Tradescantia,* but elsewhere in the chromosome the distribution of breaks was at random.

In *Crepis,* there is no karyotype made up of equal-sized, equal-armed chromosomes, corresponding to Levitsky's primitive type, the closest approximation being found in the more primitive related genera of *Prenanthes* and *Dubyaea* (Babcock, Stebbins, and Jenkins, 1937). Within *Crepis* itself, there is a distinct tendency for the primitive species to have more symmetrical karyotypes than the advanced species (see figs. 1–24). The primitive six-paired species have some large median chromosomes and the chromosomes of a set are not very different in total length. The four- and five-paired species have more asymmetrical chromosomes and more small median chromosomes. The latter, according to the investigations of Tobgy (1943) and Sherman (unpublished) and in conformity with the dislocation hypothesis (Navashin, 1932), are involved in the decrease of chromosome number. In the more primitive six-paired species, the satellite is usually situated on a median or a subterminal chromosome, which has a short arm several times its diameter in length; while in the great majority of four-paired species the satellite is situated on a chromosome with a short arm in the form of a spherical head. This condition is to be expected on the basis of the random occurrence of breaks: the frequency of breaks will be directly proportional to the length of the chromosome arm, small arms will have fewer breaks, and the smallest arms will be the most stable.

Navashin and Gerassimova (1935), on the basis of their experience with translocations induced by storing seed, found that it was impossible to set up a "phylogenetic" sequence on the basis of chromosome lengths and, further, it was impossible to homologize chromosomes on the basis of their morphological similarities. That is, the transition from a symmetrical to a very asymmetrical karyotype may be the result of a few or a great many translocations, and from the appearance of the karyotype we have no clue as to the number of translocations involved in its derivation. The evidence presented in this paper also demonstrates that it is impossible to build up a phylogenetic sequence on the basis of karyotype asymmetry. However, in general, the more primitive species in the genus have more symmetrical karyotypes than the more advanced species.

DECREASE IN CHROMOSOME SIZE

In the discussion of the sections it was pointed out that the primitive perennials with basic numbers of five and six have, in general, a greater total chromosome size, that is, greater chromatin content, than the more advanced annuals with basic numbers of four and three. However, as was noted by Babcock and Cameron (1934), both increase and decrease in chromosome size have occurred in the evolution of the genus. That is, unlike the progressive decrease in chromosome number, the decrease in chromatin content does not follow a strict phylogenetic sequence. In this respect, it resembles the trend toward increasing asymmetry, in which there are also exceptions to changes in a single direction.

evolutionary advancement; furthermore he also noted a correlation between chromosome size (chromatin content) and plant size. Babcock and Cameron (1934) found a similar general tendency for reduction in chromosome size with concurrent reduction or specialization of the plant organs, but at the same time pointed out that there were numerous exceptions. Avdulov (1931) postulated an evolutionary increase in total chromatin content in the grasses and linked this increase with a progressive cooling of the climate. In the evolutionary history of *Crepis*, on the other hand, there has been an important migration from a cool-temperate climate to that of warmer regions coupled with a general tendency for a decrease in chromosome size. This decrease in size would be the converse of Avdulov's hypothesis. However, all the changes in chromatin content in *Crepis* cannot be satisfactorily explained even by the joint action of the processes postulated by Avdulov and Delaunay.

The total chromosome size, or chromatin volume, may vary due to: (1) changes in genic content or total number of genes, or (2) different developmental conditions, related either to changes in the environment or to changes in specific genes. In the former case changes in genic content will be confined to specific chromosomes and will be due to the presence of either duplications or deficiencies. It has been pointed out above that large duplications or deficiencies are rather unlikely causes of karyotype alterations in *Crepis* since they usually lead to gene unbalance. Moreover, it is hardly conceivable that the evolutionary decrease in chromosome size is due to loss of genes—the difference in chromatin content between *C. neglecta* and *C. fuliginosa* is much larger than the known small deficiency in the latter species (Tobgy, 1943). The fact that the chromosomes of any one species are of the same width and that there are width differences between the species, suggests that general size differences, affecting all the chromosomes of a set, are very largely due to causes other than differences in genic content. Such general size differences may be regarded as different degrees of contraction or coiling of the "gene string." The larger part of the evolutionary decrease in *Crepis* chromosomes may be attributed to different developmental conditions, that is, to gene-determined physiological differences between the species.

It has been demonstrated that profound alterations in chromosome size may be produced by a variety of agents, such as: low temperature (Delaunay, 1930, 1931), excess or deficiency of phosphorus (Pierce, 1937), chloral hydrate (Kagawa, 1929), and the action of specific genes (Lesley and Frost, 1927; Navashin, 1934; Darlington, 1937, p. 53). Consequently it is unlikely that evolutionary size changes in chromosomes can be ascribed to one or a few causes as suggested by Delaunay and Avdulov. Undoubtedly, variations in size in *Crepis* chromosomes can be related to the different physiological states of the species, but it will be necessary to have a clearer understanding of chromosome biochemistry before specific causes of size changes can be properly analyzed.

SUMMARY

1. The chromosome numbers of 113 species, representing 23 of the 27 sections of *Crepis*, are reported and their karyotypes illustrated.

2. The following general trends in karyotype evolution in this genus are noted: (a) decrease in chromosome number; (b) increase in asymmetry of the chromosomes; (c) decrease in chromosome size. These trends in karyotype evolution have occurred independently of processes resulting in morphological change in the plant.

3. Decrease in chromosome number has been progressive, from $n = 6$ to $n = 3$. The process went on step by step, through the loss of one chromosome at a time; and each step occurred independently on several different occasions. The evidence from *Crepis* supports Navashin's dislocation hypothesis; that is, change in chromosome number through reciprocal translocations. In addition to the main trend of decrease in number, there have also been increases in number in certain restricted groups, such as amphidiploid hybrids and polyploids of various types.

4. Chromosome asymmetry is a further consequence of unequal reciprocal translocation, in spite of the fact that the process does produce an opposite trend toward symmetry, once the initial asymmetry is established. In the long run the latter tendency predominates to a greater or less degree. Although it is impossible in *Crepis* to recognize a phylogenetic sequence on the basis of chromosome asymmetry, yet in general the more primitive species in the genus have more symmetrical chromosomes than the more advanced species.

5. The decreasing trend in chromosome size also fails to follow a strict phylogenetic sequence. Although there is a general tendency for reduction in chromosome size with concurrent reduction or specialization of the plants; yet at the same time there are numerous exceptions. The factors influencing this trend in *Crepis* are evidently complex, since they may reflect different physiological states which in turn may be influenced by various environmental factors. But it may be assumed that the physiological differences which characterize the species are gene determined; and therefore gene mutations may furnish the basis for the trend in decreasing chromosome size.

TABLES

EXPLANATION OF SYMBOLS

† Species or accessions examined for the first time, or a new drawing. The letters following the accession numbers indicate the previously published reports of the respective accessions as follows:

C = Babcock, E. B., and Cameron, D. R., 1934.
Ca = Cameron, D. R., 1934.
H = Hollingshead, L., and Babcock, E. B., 1930.
J = Babcock, E. B., Stebbins, G. L., Jr., and Jenkins, J. A., 1937.
L = Babcock, E. B., and Lesley, M. M., 1926.
M = Mann, M. C., 1925.
S = Babcock, E. B., and Stebbins, G. L., Jr., 1938.

The numbers following the letters in the column entitled "Published illustration" refer to pages in previous publications where illustrations are to be found. The letters have the same significance as above.

! Previously published drawing used in the present paper.

? Some question as to the accuracy of the count, due to the large number of chromosomes and limited material available.

[Determination in doubt]—When these plants were collected they were in a condition unsuitable for herbarium specimens, and therefore could not be reclassified in Babcock and Stebbins, The American Species of Crepis (1938).

TABLE 1

THE SOMATIC CHROMOSOME NUMBERS OF ONE HUNDRED AND THIRTEEN SPECIES OF CREPIS

Species	Somatic chromosome number	Accession number	Published illustration	Section number
C. aculeata (DC.) Boiss.	8	1602 H	H15. C319 !	26
C. acuminata Nutt. ssp. *typica* Babc. et Stebbins	22	S1864 SJ		15
	22	S1869 SJ		
	33	1922 HS		
	33	2096 HS		
	33?	S2163 J		
	44?	1778 HS	H26.	
C. albida Vill. ssp. *asturica* (Lacaita et Pau) Babc. [H. as *C. asturica* Lacaita]	10	2088 HC	H12. C316 !	7
C. albida Vill. ssp. *macrocephala* (Willk.) Babc.	10	2957 C		
**C. albiflora* Babc.	8	3312 *	*	4
C. alpestris (Jacq.) Tausch	8	2512 C	C303 !	8
	8	3401 *		
**C. apula* (Fiori) Babc.	8	3474 *	*	24
C. alpina L.	10	1020 M	M.	20
	10	1499 H	H13. C316 !	
	10	1640 Ca		
	10	1641 Ca		
	10	2769 Ca		
	10	2783 Ca		
C. amplexifolia (Godr.) Willk.	8	1019 MLH	M. H15. C319 !	26
	8	1224 ML		
	8	3199 *		
	8	3201 *		
C. aspera L.	8	1018 M	M.	26
	8	1142 M		
	8	1227 M		
	8	1135 H	H14. C319 !	
	8	1973 H		
[C. as *C. aspera jordanensis*]	8	3010 C		
	8	2497 *		
	8	3148 *		
	8	3149 *		
	8	3161 *		

TABLE 1—*Continued*

Species	Somatic chromosome number	Accession number	Published illustration	Section number
C. atribarba Heller ssp. *originalis* Babc. et Stebbins				15
[H. as *C. gracilis* (Eat.) Rydb.]	22	2572 HS	H26.	
	44	3406 S		
[H. as *C. gracilis* (Eat.) Rydb. accession No. 1695]	55?	1965 HS		
[H. as *C. barbigera* Leiberg—determination in doubt]	88?	1959 H		
C. aurea (L.) Cass. ssp. *typica* Babc.	10	1021 M		4
	10	1061 M	M.	
	10	1098 M		
	10	2170 H	H18. C301 !	
C. aurea (L.) Cass. ssp. *lucida* (Ten.) Babc.	10	2912 C		
C. Bakeri Greene ssp. *typica* Babc. et Stebbins	43–46	3402 S		15
C. Bakeri Greene ssp. *Cusickii* (Eastw.) Babc. et Stebbins [H. as *C. occidentalis* Nutt. form]	22?	2220 HS		
	22	S2331 S		
**C. Baldaccii* Hal.	10	3417 *	*	10
C. barbigera Leiberg	44	1838 HS		15
[determination in doubt]	88?	1840 HS		
	88?	1842 HS	H26.	
	88?	3404 S		
C. bellidifolia Loisel.	8	2921 C	C319 !	27
C. biennis L.	40	1056 M	M.	10
	38–42	1878 H	H20.	
	39	3444 *		
C. bithynica Boiss.	10	3218 C	C305 !	11
C. blattarioides (L.) Vill.	8	1069 M	M.	6
	8	2033 H	H17. C303 !	
**C. Bourgeauii* Babc.	8	3475 *	*	25
C. Bungei Ledeb.	8	1827 H	H18. C304 !	14
C. bursifolia L.	8	1000 M	M.	27
	8	1220 H	H14. C319 !	
C. canariensis (Sch. Bip.) Babc.	8	3049 C	C317 !	25

TABLE 1—*Continued*

Species	Somatic chromosome number	Accession number	Published illustration	Section number
C. capillaris (L.) Wallr.	6	899 M } H	H19. C311 !	24
	6	900 M		
	6	1042 M	M.	
	6	1132 M		
	6	1158 M		
	6	982 H		
	6	2683 H		
	6	X H		
C. chondrilloides Jacq.	8	1601 L		10
	8	1907 H	H22. C306 !	
	8	2180 H		
C. chrysantha (Ledeb.) Froel.	8	2179 H	H17. C303 !	4
C. ciliata C. Koch.	40	1601 L		10
	40, 42?	2181 H	H20.	
C. Clausonis (Pomel) Batt. et Trab.	8	2848 C	C317 !	25
C. conyzaefolia (Gouan) Dalla Torre				6
	8	1060 M		
[M. as *C. grandiflora* Tausch]	8	1097 M	M.	
	8	1187 M } L		
	8	2183 H	H17. C303 !	
**C. corymbosa* Ten.	8	3060 *	*	24
C. cretica Boiss.	8	2869 C	C311. *	24
C. crocea (Lam.) Babc.				11
[H. as *C. Bungei* Ledeb.]	16	2174 HC	H18.	
	16	2352 C	C304 !	
	16	2353 C		
C. Dioscoridis L. ssp. *typica* Babc.	8	1005 M		23
	8	1007 M		
	8	1028 M	M.	
	8	1070 M		
	8	1085 M		
	8	972 M } H		
	8	1455 H	H22. C306 !	
	8	1742 H		
	8	3446 *		
C. Dioscoridis L. ssp. *argolica* Babc. [C. as *C. argolica*]	8	2884 C	C306.	
C. Dioscoridis L. ssp. *tirynthica* Babc. [C. as *C. argolica tirynica*]	8	3036 C		

TABLE 1—*Continued*

Species	Somatic chromosome number	Accession number	Published illustration	Section number
C. Dioscoridis L. ssp. *tubaeformis* (Hal.) Babc. [C. as *C. tubaeformis* Halacsy]	8	3066 C		
	8	3069 C	C306.	
C. divaricata (Lowe) F. Sch.	8	2980 C	C317 !	25
C. elegans Hook.	14	2654 H	H21. C314 !	12
C. eritreënsis Babc.	10	3005 C	C316. *	20
C. flexuosa (DC.) Benth. et Hook.f.	14	2983 C	C314 !	12
C. foetida L. ssp. *vulgaris* (Bisch.) Babc.	10	1050 M	M.	20
	10	1063 M		
	10	1075 M		
	10	1236 M		
	10	1536 M		
	10	1542 M		
	10	1569 M		
	10	1751 H	H12. C316 !	
	10	2188 H	H12.	
	10	2048 H	H12.	
	10	2307 H		
	10	2047 *		
C. foetida L. ssp. *commutata* (Spr.) Babc. [H. as *Rodigia commutata* Spr.]	10	1666 H		
	10	2219 H	H12. C316 !	
C. foetida L. ssp. *rhoeadifolia* (Bieb.) Schinz et Keller	10	2318		
C. Fontiana Babc.	8	3225 C	C317 !	25
C. fuliginosa Sibth. et Sm.	6	2891 C		24
	6	2994 C		
	6	3043 C	C311 !	
	6	3460 *		
**C. geracioides* Hausskn.	12	3456 *	*	1
C. gymnopus Koidz.	8	2746 H	H24. C309 !	13
C. hierosolymitana Boiss.	12	2619 H	H20. C312 !	5
C. hokkaidoensis Babc. [H. as *C. burejensis* F. Schmidt]	8	2747 H	H17. C303 !	4
C. Hookeriana J. Ball	8	1458 LH	H18. C303 !	11

TABLE 1—*Continued*

Species	Somatic chromosome number	Accession number	Published illustration	Section number
C. hypochaeridea (DC.) Thell. ssp. *rhodesica* Babc.	8	3059 C	C303.	8
C. hypochaeridea (DC.) Thell. ssp. *brevicaulis* Babc.	8	3399 *	*	
C. incana Sibth. et Sm.	16	1667 H	H23. C306 !	10
C. incarnata (Wulf.) Tausch	8	1304 MH	M. H24. C309 !	13
C. intermedia Gray				15
[H. as *C. acuminata* Nutt. form—determination in doubt]	33	1848 HS		
	33	1919 HS		
	33	1934 HS		
	44?	3286 S		
	44?	3289 S		
	44?	S1700 J		
	44?	S2173 J		
	55?	3224 S		
	55?	S2499 SJ		
[C. as *C. atribarba* Heller—determination in doubt]	88?	3045 CS		
**C. Jacquini* Tausch	12	3467 *	*	4
C. juvenalis (Delile) F. Sch.	8	3205 C	C319 !	26
	8	3206 C		
	8	3207 C		
C. kashmirica Babc.	12	3186 C	*	2
**C. kilimandscharica* O. Hoffm.	8	3280 *	*	8
C. Kotschyana Boiss.				20
[H. as *C. Bureniana* Boiss.]	8	1655 H	H15. C316 !	
	8	2340 *		
**C. lapsanoides* [*lampsanoides*] (Gouan) Tausch	12	3466 *	*	5
C. latialis Sebast.				10
[H. as *C. lacera* Ten.]	8	1914 H	H22. C306 !	
C. leontodontoides All.	10	1807 H	H19. C305 !	9
C. lybica (Pamp.) Babc.	8	1698 H	H15. C317 !	25
	8	3389 *		
C. lyrata Froel.	12	1644 MH	H20. C312 !	5

TABLE 1—*Continued*

Species	Somatic chromosome number	Accession number	Published illustration	Section number
C. modocensis Greene ssp. *typica* Babc. et Stebbins	44	S2254 S		15
C. modocensis Greene ssp. *subacaulis* (Kell.) Babc. et Stebbins [H. as *C. scopulorum* Cov.]	44?	2773 HS		
	44?	S2159 SJ		
	55 or 66	S2158 J		
C. Marschallii (C. A. Mey.) F. Sch.	8	1532 H	H15. *	25
C. mollis (Jacq.) Asch.	12	1614 L		5
	12	2201 H	H20. C312 !	
	12	3219 *		
C. montana Urv. [M. as *C. Sieberi* Boiss.]	12	1175 MH	M. H20. C312 !	5
C. monticola Cov.	22	S3261 *		15
	22	S1973 SJ		
	44	.... SJ		
	55?	2771 HS	H25.	
C. multicaulis Ledeb. ssp. *genuina* (Rgl.) Babc. [H. as *C. multicaulis* Ledeb.]	10	1480 H	H19. C305 !	21
C. multicaulis Ledeb. ssp. *congesta* (Rgl.) Babc.	10	3187 C		
C. multiflora Sibth. et Sm.	8	3062 C	C306 !	23
C. Mungierii Boiss.	12	2870 C		5
	12	2876 C		
	12	2877 C	C312 !	
C. nana Richards.	14	2698 H	H21. C314 !	12
C. neglecta L.	8	1024 M		24
	8	1134 M	M.	
	8	1521 M		
	8	1753 H	H19. C311 !	
	8	2335 *		
	8	3462 *		
**C. Newii* Oliver et Hiern ssp. *Greenwayi* Babc.	8	3274 *	*	8
C. nicaeënsis Balb.	8	2700 H	H19. C311 !	24
	8	3425 *		
C. nigricans Viv.	8	3020 C	C319 !	27

TABLE 1—*Continued*

Species	Somatic chromosome number	Accession number	Published illustration	Section number
C. Noronhaea Babc.				25
[C. as *C. pumila* (Lowe)]	8	3022 C	*	
C. occidentalis Nutt. ssp. *typica* Babc. et Stebbins	22	2772 HS	H25.	15
	22	S1671 SJ		
	22	S2170 SJ		
	33	3285 S		
	33	3288 S		
	33	S2117 SJ		
	33	S2182 S		
	33	S2302 S		
	33?	S2367 S		
	44	S2169 SJ		
C. occidentalis Nutt. ssp. *costata* (Gray) Babc. et Stebbins	44	1921 H	H25.	
C. occidentalis Nutt. ssp. *pumila* (Rydb.) Babc. et Stebbins	33	3403 S		
	77?	S.... SJ		
C. occidentalis Nutt. ssp. *conjuncta* (Jepson) Babc. et Stebbins	44	S1589 S		
**C. oporinoides* Boiss.	8	3398 *	*	10
C. oreades Schrenk	8	2981 C	C304!	11
C. palaestina (Boiss.) Bornm.	8	1552 MH	M. H24. C309!	19
	8	3156 *		
	8	3431 *		
C. paludosa (L.) Moench	12	1822 L		1
	12	1825 H	H17. C301!	
C. pannonica (Jacq.) K. Koch				10
[L. as *C. Blavii* Asch.]	8	1236 L		
	8	1695 H	H22. C306!	
	8	3450 *		
C. parviflora Desf.	8	1234 M	M.	24
	8	1533 M		
	8	1630 H	H19. C311!	
	8	2287 *		
	8	3099 *		
C. patula Poir.	8	2839 C	C306!	23

TABLE 1—*Continued*

Species	Somatic chromosome number	Accession number	Published illustration	Section number
C. pleurocarpa Gray	22	S2462 S		15
[H. as *C. acuminata* form—determination in doubt]	55?	1830 HS	H26.	
	55	S1975 J		
	55?	S1976 J		
C. polytricha (Ledeb.) Turcz.	16	2562 C	C303 !	4
C. pontana (L.) Dalla Torre	10	2204 H	H16. C301 !	6
	10	3437 *		
C. praemorsa (L.) Tausch	8	2133 H	H24. C309 !	13
C. pterothecoides Boiss.	8	3232 C	C309 !	19
C. pulchra L. ssp. *typica* Babc.	8	996 M	M.	19
	8	1073 M		
	8	1143 M		
	8	1213 M H	H24.	
	8	1483 H	H24. C309 !	
[C. as *C. granatensis*]	8	1894 HC	C309.	
C. pulchra L. ssp. *africana* Babc.	8	2963 *		
C. pulchra L. ssp. *turkestanica* Babc.	8	2370 *		
	8	2371 *		
	8	2566 *		
C. pygmaea L.	12	1530 L		3
	12	3251 C	C312 !	
C. Raulini Boiss.	10	2875 C	C305 !	10
C. Reuteriana Boiss. ssp. *typica* Babc.	8	2134 H		19
	8	2218 H	H24. C309 !	
[C. as *C. Reuteriana* fa. *hirta*]	8	3134 C		
C. Reuteriana Boiss. ssp. *Eigiana* Babc. [C. as *C. Eigiana*]	8	3125 C		
	8	3138 C	C309.	
C. Robertioides Boiss.	8	3128 *		11
	8	3129 C	C311 !	
C. rubra L.	10	1032 M	M.	20
	10	1110 M		
	10	1111 M		
	10	1506 H	H14.	
	10	1176 H	H14. C316.	
	10	2888 *		
	10	2995 *	*	
	10	3452 *	*	

TABLE 1—*Continued*

Species	Somatic chromosome number	Accession number	Published illustration	Section number
C. runcinata (James) T. et G. ssp. *typica* Babc. et Stebbins	22	2065 H	H27.	15
	22	2066 H		
	22	2068 H		
	22	2069 H		
	22	2071 H		
	22	2075 H		
	22	2076 H		
	22	2077 H		
	22	2078 H		
	22	2083 H		
C. runcinata (James) T. et G. ssp. *Andersonii* (Gray) Babc. et Stebbins [H. as *C. Andersoni* Gray]	22	2086 H	H27.	
C. runcinata (James) T. et G. ssp. *glauca* (Nutt.) Babc. et Stebbins [H. as *C. glauca* (Nutt.) T. et G.]	22	2079 H	H27.	
C. runcinata (James) T. et G. ssp. *hispidulosa* (Howell) Babc. et Stebbins	22	1829 H	H27.	
C. runcinata (James) T. et G. ssp. *Hallii* Babc. et Stebbins [H. as *C. Andersoni* Gray]	22	2136 H	H27.	
C. sancta (L.) Babc. ssp. *bifida* (Vis.) Thell.				22
[C. as *C. bifida* (Vis.) F. et M.]	10	3057 C		
	10	3083 C		
	10	3084 C		
	10	3087 C	C305 !	
C. sancta (L.) Babc. ssp. *nemausensis* (Gouan) Thell. [H. as *Pterotheca sancta* (L.) K. Koch]	10	2582 H	H22.	
	10	2583 H		
[C. as *C. sancta beirutica*]	10	3160 C	C305 !	
	10	3088 *		
	10	3090 *		
**C. scaposa* R.E. Fr. ssp. *taraxaciformis* (R.E. Fr.) Babc.	8	3301 *	*	8
**C. Schachtii* Babc.	10	3240 *	*	11
C. senecioides Delile				27
[M. as *C. breviflora* Delile]	8	1044 MH	M.	
	8	2061 H	H14. C319 !	
C. setosa Hall. f. ssp. *typica* Babc.	8	1017 M	M.	26
	8	1036 M H	H14. C319 !	
	8	1510 H		
C. setosa Hall. f. ssp. *Topaliana* Babc.	8	2906 C		

TABLE 1—*Continued*

Species	Somatic chromosome number	Accession number	Published illustration	Section number
C. sibirica L.	10	1033 M	M.	1
	10	1072 M		
	10	1225 M		
	10	1862 H	H16. C301 !	
C. Stojanovi Georg.	8	3176 C	C309 !	19
C. suberostris Coss. et Durieu ssp. *typica* Babc.	10	2829 C	C305 !	9
C. Suffreniana (DC.) Lloyd	8	2975 C	C311 !	24
**C. suffruticosa* Babc.	8	3281 *	*	8
C. syriaca (Bornm.) Babc.				20
[H. as *C. alpina* var. *syriaca* Bornm.]	10–13	1923 H	H13. C316 !	
	10–18	1923 Ca	Ca 260–261.	
	10	3106 Ca	Ca 260.	
	10	3132 Ca		
	10	3158 Ca		
	11–12	3159 Ca		
	10	3167 Ca		
	10	3168 Ca		
C. taygetica Babc.	40	2893 C		10
C. tectorum L.	8	1067 M	M.	14
	8	1084 M		
	8	1498 H	H19. C311 !	
	8	1702 H		
**C. terglouensis* (Hacq.) A. Kern.	12	3414 *	*	4
C. Thomsonii Babc.	10	3208 C	C316 !	20
C. tingitana Salz.	10	1574 L		9
	10	1681 H	H18. C305 !	
C. Triasii (Camb.) Fries	8	2945 C	C317 !	10
	8	2949 C		
C. vesicaria L. ssp. *typica* (Fiori) Babc.	8	1576 MH	M. H15.	25
	8	2865 *		
	9	3009 *		
	8	3200 *		
	8	3236 *	C317. *	
	16	2851 C		
	16	2852 C		
	16	2853 C		
	16	2854 C		
	16	2947 C		
	16	2948 C	*	
	16	3056 C		

TABLE 1—*Concluded*

Species	Somatic chromosome number	Accession number	Published illustration	Section number
[C. as *C. taraxacoides* Desf.]	16	2944 C	C317.	
C. vesicaria L. ssp. *andryaloides* (Lowe) Babc.	8	2817 C	C317 !	
[C. as *C. hieracioides* Lowe]	8	2818 C		
	8	2823 C		
C. vesicaria L. ssp. *hyemalis* (Biv.) Babc.				
[C. as *C. hyemalis* (Biv.) C.P. et G.]	8	3053 C	C317 !	
C. vesicaria L. ssp. *myriocephala* (Coss. et DR.) Babc.	8	1040 M	M.	
[M., H. as *C. myriocephala* Coss. et DR.]	8	1557 M H	H15. C317.	
	8	2840 *	*	
	8	2841 *		
[C. as *C. myriocephala* Coss. et DR.]	16	2844 C	*	
	16	2845 C		
C. vesicaria L. ssp. *stellata* (Ball) Babc.	9	2831 *		
	9–12	2832 *		
	8	2834 *		
	8	2837 *		
	8	2843 *		
	8	2847 *	*	
	16	2827 *		
	16	2836 *		
	16	3473 *	*	
C. vesicaria L. ssp. *taraxacifolia* (Thuill.) Thell.	8	998 M		
	8	1572 M	M.	
[M., H. as *C. taraxacifolia* Thuill.]	8	1064 M H	H15. C317 !	
	8	1704 H		
	8	1806 H		
	8	1895 H		
	8	2812 *		
	8	2825 *		
	8	2838 *		
	8	2803 C		
[C. as *C. taraxacifolia laciniata* (Lowe)]	8	2815 C		
	8	2819 C		
[H. as *C. Hackeli* Lange]	16	1873 H	H15. C317. *	
	16	2777 *		
C. viscidula Froel.	12	3178 C	C301 !	1
C. willemetioides Boiss.	12	3217 C	C312 !	5
C. Zacintha (L.) Babc. [Navashin, 1930. *Zacyntha verrucosa* Gärtner]	6	2909 *		23
	6	3439 *	*	

TABLE 2

SPECIES PREVIOUSLY INCLUDED IN *Crepis* AND NOW REFERRED TO OTHER GENERA

Species	Publication	Accession number	Present disposition
C. bulbosa (L.) Tausch.	M* H	1046 1303	*Aetheorrhiza bulbosa* (L.) Cass.
C. bhotanica Hutchinson...... ..	C C	3216 3245	*Dubyaea hispida* (Don.) DC.
Lactuca depressa (Hook. f. et Thoms.) (*C. depressa*).......	C	3246	*Youngia depressa* (Hook. f. et Thoms.) Babc. et Stebbins
C. fuscipappa (Thw.) Benth.....	L	1198	*Youngia fuscipappa* Thwaites
Prenanthes glomerata Dcne. (*Crepis glomerata* Benth. et Hook. f.)....................	C	3252	*Soroseris glomerata* (Dcne.) Stebbins
C. japonica (L.) Benth...........	M	990	*Youngia japonica* (L.) DC. ssp. *genuina* (Hochr.) Babc. et Stebbins
C. tenuifolia Willd..............	H	1826	*Youngia tenuifolia* (Willd.) Babc. et Stebbins

* See "Explanation of Symbols," p. 275.

TABLE 3

THE FREQUENCIES OF THE VARIOUS HAPLOID CHROMOSOME NUMBERS IN THE SECTIONS OF CREPIS

Section	Haploid Chromosome Number								Total
	6	5	4	3	7	8	11	20	
1. Desiphylion	3	1	..	..	..	..	..	..	4
2. Spathoides	1	..	..	..	..	..	..	..	1
3. Omalocline	1	..	..	..	..	..	..	..	1
4. Brachypodes	2	1	3	..	..	1	..	..	7
5. Mesomeris	7	..	..	..	..	..	..	..	7
6. Soyeria	..	1	2	..	..	..	..	..	3
7. Paleya	..	1	..	..	..	..	..	..	1
8. Anisorhamphus	..	..	6	..	..	..	..	..	6
9. Gephyroides	..	3	..	..	..	..	..	..	3
10. Berinea	..	2	5	..	..	1	..	3	11
11. Macropodes	..	2	3	..	..	1	..	..	6
12. Ixeridopsis	..	..	..	..	3	..	..	..	3
13. Intybellia	..	..	3	..	..	..	..	..	3
14. Mesophylion	..	..	2	..	..	..	..	..	2
15. Psilochaenia	..	..	..	..	..	..	10*	..	10
19. Phaecasium	..	..	5	..	..	..	..	..	5
20. Hostia	..	6†	1	..	..	..	..	..	7
21. Microcephalum	..	1	..	..	..	..	..	..	1
22. Pterotheca	..	1	..	..	..	..	..	..	1
23. Zacintha	..	..	3	1	..	..	..	..	4
24. Phytodesia	..	..	7	2	..	..	..	..	9
25. Lepidoseris	..	..	9‡	..	..	..	..	..	9
26. Nemauchenes	..	..	5	..	..	..	..	..	5
27. Psammoseris	..	..	4	..	..	..	..	..	4
Total	14	19	58	3	3	3	10	3	113

* Section Psilochaenia includes all of the western American species which are polyploids on the basis of 11.

† One of these species, *C. syriaca*, sometimes has more than 5 pairs of chromosomes.

‡ One species of Lepidoseris, *C. vesicaria*, has both diploid ($n=4$) and tetraploid ($n=8$) forms.

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CHROMOSOME NUMBERS IN THE HYDROPHYLLACEAE: II

BY

MARION S. CAVE AND LINCOLN CONSTANCE

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CHROMOSOME NUMBERS IN THE HYDROPHYLLACEAE : II

BY

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IN THE FORMER PAPER of this series* chromosome numbers were put on record for forty-six species and varieties of *Emmenanthe*, *Eucrypta*, *Hydrophyllum*, *Nemophila*, *Phacelia*, *Pholistoma*, and *Romanzoffia*. The purpose of the present paper is to supplement this list with counts of twenty additional entities in *Eucrypta* and *Phacelia*, as well as to give confirmatory results from different geographical populations of forms whose counts have been published previously.

As before, all counts have been made by smearing young anthers in acetocarmine. Every count is referable to a specimen deposited in the University of California Herbarium. Because of the difficulty of field work at the present time, buds of several species were obtained by growing the plants from seed. The writers anticipate that continuance of this project will, in the near future, necessarily have to depend upon material obtained in this manner, and they are therefore especially desirous of securing viable seed of as many cytologically uninvestigated species of the family as possible.

We wish to express our sincere thanks to the correspondents who have already generously supplied us with much of the material used in the present paper. Their names, for the most part, appear as collectors in table 1, but we are grateful also to those who furnished buds or seeds which we were unable to use.

The occurrence of a species with ten pairs of chromosomes in *Eucrypta* and of a species with twelve pairs in *Phacelia* has not hitherto been reported. There are now known to occur in *Phacelia* the numbers eight, nine, ten, eleven, twelve, thirteen, and twenty-two. The eleven-paired species are considerably more numerous than any of those having other numbers, they occur in four of the five sections for which counts are available, and they include all the perennials thus far investigated (with the exception of those polyploid forms having multiples of eleven). The discovery that *P. Lemmoni*, a desert annual, has twenty-two pairs is the first record of this number outside the *P. magellanica-heterophylla-californica* polyploid complex, and points to the possible existence of a second polyploid complex not previously suspected.

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* University of California Publications in Botany, vol. 18, no. 9.

FIGURE A

Chromosomes of Phacelia. × 1150.

1. *P. Bolanderi,* II M; *Constance and Rollins* 2999.
2. *P. Davidsonii,* Interk.; *Constance and Peirson* 2847.
3. *P. Lemmoni,* II M; *K. H. Beach* 1001.
4. *P. linearis,* II M; *Constance and Beetle* 2706.
5. *P. verna,* I M; *Constance and Rollins* 2955.
6. *P. grandiflora,* II M; *W. C. McCalla* 6053.
7. *P. longipes,* I M; *J. F. Ashley.*
8. *P. cicutaria,* II T; *A. A. Beetle* 3018.
9. *P. congesta* var. *rupestris,* I M; *E. Sublett* T1286.
10. *P. crenulata* var. *ambigua,* II M; *F. W. Gould* 1470.
11. *P. cryptantha,* II M; *H. Lewis* 1604.
12. *P. Palmeri* var. *foetida,* II M; *F. W. Gould* 1581.
13. *P. pedicellata,* I M; *Lewis and Epling* 1601.
14. *P. Popei,* I M; *O. E. Sperry* T1042.
15. *P. ramosissima,* I A; *Stebbins and Beetle* 3251.

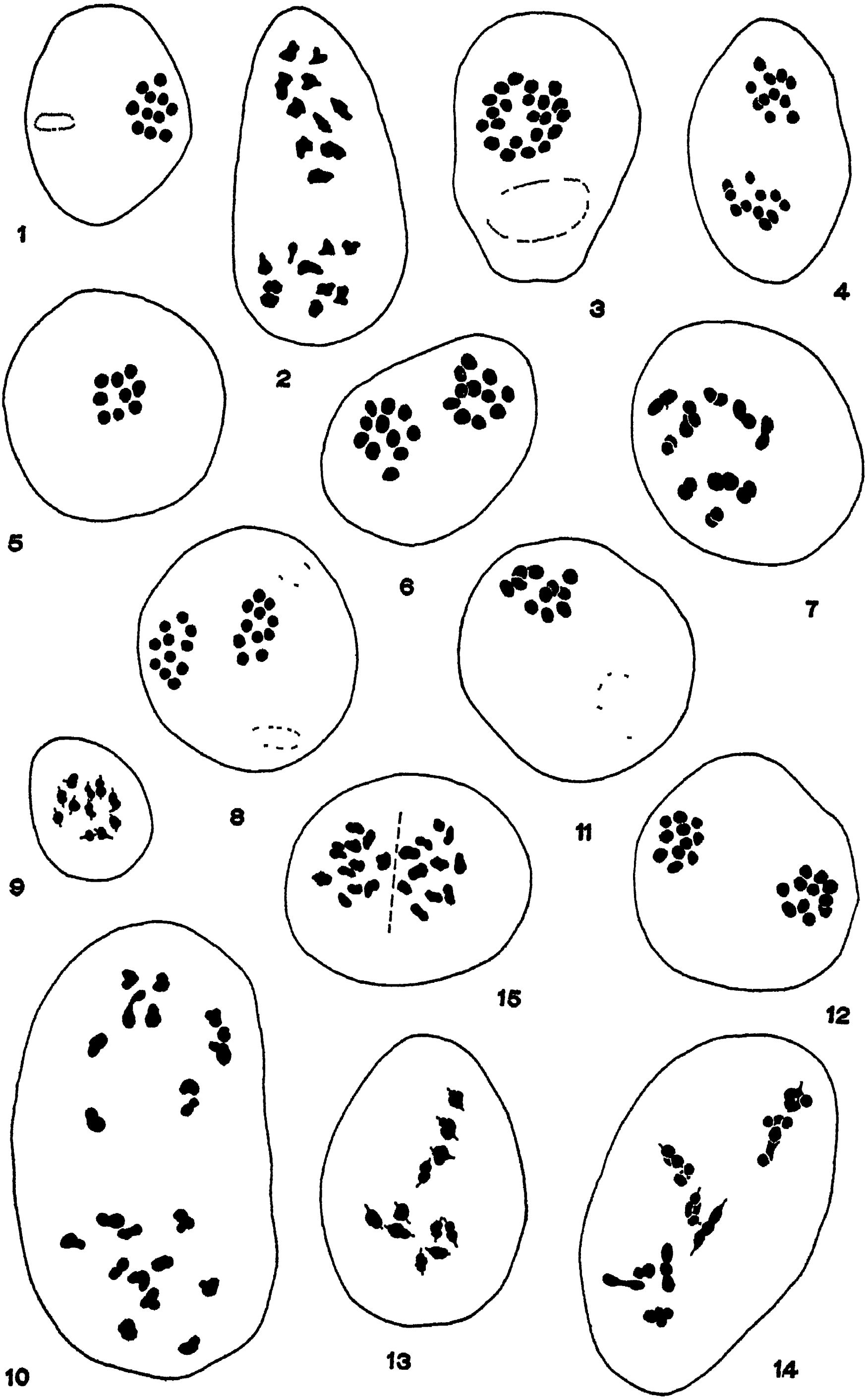

Figure A

FIGURE B

Chromosomes of Phacelia and Eucrypta. × 1150.

16. *P. californica* var. ?, Diak.; *Constance and Rollins* 2900.
17. *P. californica* var. *jacintensis*, Diak.; *H. Lewis* 1709.
18. *P. imbricata,* I A; *W. S. Boyle* 1069.
19. *P. leucophylla,* II M; *Constance and Rollins* 2956.
20. *P. leucophylla* var. ?, Diak.; *R. C. Rollins* 3029.
21. *P. nemoralis*, Diak.; *W. S. Boyle* 1086.
22. *P. virgata,* II M; *Constance and Rollins* 2927.
23. *P. virgata* var. *bernardina ?*, II M; *H. Lewis* 1718.
24. *P. brachyloba*, Diak.; *H. Lewis* 1710.
25. *P. Fremontii,* II M; *F. W. Gould* 1652.
26. *E. chrysanthemifolia,* I A; *Constance and Boyle* 2860.
27. *E. chrysanthemifolia* var. *bipinnatifida,* I A; *Lewis and Epling* 1607.

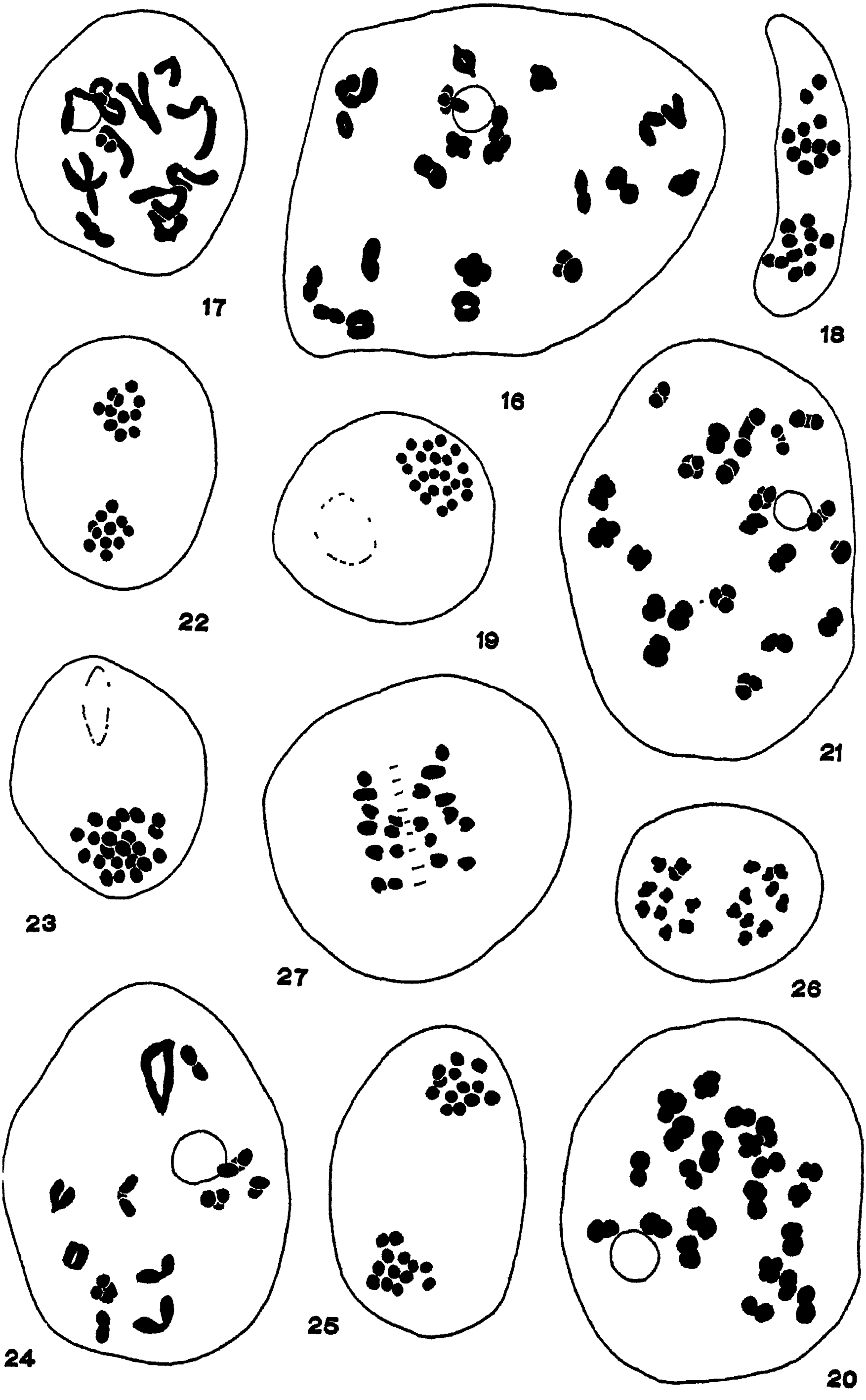

Figure B

TABLE 1

CHROMOSOME NUMBERS IN THE HYDROPHYLLACEAE

Name	n number	Locality	Collector
Eucrypta chrysanthemifolia (Benth.) Greene	10	Alum Rock Creek, Santa Clara Co., Calif.	*Constance and Boyle* 2860
	10	Niles, Alameda Co., Calif.	*Constance* 2236
var. *bipinnatifida* (Torr.) Const.	10	Split Rock Tank, Riverside Co., Calif.	*Lewis and Epling* 1607
Phacelia			
Section Gymnobythus			
grandiflora (Benth.) Gray	11	La Jolla, San Diego Co., Calif.	*W. C. McCalla* 6053
Section Whitlavia			
longipes Torr.	11	Mono Basin, Santa Barbara Co., Calif.	*J. F. Ashley*
	11	Frenchman Flats, Los Angeles Co., Calif.	*Lewis and Dunn* 1713
Section Euphacelia			
cicutaria Greene	11	Tehachapi Mountains, Kern Co., Calif.	*A. A. Beetle* 3018
	11	Kern River Canyon, Kern Co., Calif.	*Lewis, Epling, and Mehlquist* 1596
congesta Hook. var. *rupestris* (Greene) Macbr.	11	Brewster, Alpine Co., Texas	*E. Sublett* T1286
crenulata Torr. var. *ambigua* (Jones) Macbr.	11	Black Hill, Washington Co., Utah	*F. W. Gould* 1470
cryptantha Greene	11	Piñon Flats, Riverside Co., Calif.	*H. Lewis* 1604
Palmeri Torr. var. *foetida* (Goodd.) Brand	11	St. George, Washington Co., Utah	*F. W. Gould* 1581
pedicellata Gray	11	Nightingale, Riverside Co., Calif.	*Lewis and Epling* 1601
Popei Torr. and Gray	11	Brewster, Alpine Co., Texas	*O. E. Sperry* T1042
ramosissima Dougl.	11	Gazelle, Siskiyou Co., Calif.	*Stebbins and Beetle* 3251
magellanica-californica-heterophylla complex			
californica Cham. var. ?	22	Clear Creek, Siskiyou Co., Calif.	*Constance and Rollins* 2900
var. *jacintensis* Dundas	11	Saunders Meadows, Riverside Co., Calif.	*H. Lewis* 1709
imbricata Greene	11	Empire, Mendocino Co., Calif.	*Constance and Beetle* 2607
	11	Kern River Canyon, Kern Co., Calif.	*Lewis, Epling, and Mehlquist* 1599
	11	Napa, Napa Co., Calif.	*W. S. Boyle* 1069
leucophylla Torr.	22	Roseburg, Douglas Co., Ore.	*Constance and Rollins* 2956
var. ?	22	Lake Tahoe, Eldorado Co., Calif.	*R. C. Rollins* 3029
nemoralis Greene	22	South Fork Eel River, Humboldt Co., Calif.	*W. S. Boyle* 1086
virgata Greene	11	Hoopa Valley, Humboldt Co., Calif.	*Constance and Rollins* 2876
	11	Yreka, Siskiyou Co., Calif.	*Constance and Rollins* 2927
var. *bernardina* Greene ?	22	Cuddy Valley, Kern Co., Calif.	*H. Lewis* 1718
Section Eutoca			
Bolanderi Gray	11	Weott, Humboldt Co., Calif.	*Constance and Rollins* 2999
Davidsonii Gray	10	San Bernardino Mts., San Bernardino Co., Calif.	*Constance and Peirson* 2847
	10	Mt. Pinos, Ventura Co., Calif.	*Lewis and Dunn* 1714
Lemmoni Gray	22	Burnt Cabin Summit, Churchill Co., Nev.	*K. H. Beach* 1001
linearis (Pursh) Holz.	11	Condon, Gilliam Co., Ore.	*Constance and Beetle* 2706
	11	Galice, Josephine Co., Ore.	*Constance and Rollins* 2963
verna Howell	9	Roseburg, Douglas Co., Ore.	*Constance and Rollins* 2955
Section Microgenetes			
brachyloba (Benth.) Gray	12	Piñon Flats, Riverside Co., Calif.	*H. Lewis* 1710
Fremontii Torr.	13	Diamond Valley, Washington Co., Utah	*F. W. Gould* 1652

REVIEW OF THE ACROCHAETIUM-RHODOCHORTON COMPLEX OF THE RED ALGAE

BY

GEORGE F. PAPENFUSS

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REVIEW OF THE ACROCHAETIUM-RHODOCHORTON COMPLEX OF THE RED ALGAE

BY

GEORGE F. PAPENFUSS

IN THE identification of species of *Acrochaetium*, the phycologist is faced not only by the possibility of overlooking some of the fifty-odd new species which have been published since the appearance of Hamel's monograph of the genus in 1928, but also by the problem of whether to use the generic name *Acrochaetium* Nägeli (1861), *Rhodochorton* Nägeli (1861), or *Audouinella* Bory (1823).

Although *Acrochaetium* and *Rhodochorton* have been considered distinct genera by the majority of investigators, several writers, including Setchell and Gardner (1930), Rosenvinge (1935), Nakamura (1941), and Dawson (1944), have accepted the contention of Drew (1928) that these genera are linked by so many intermediate species that it would be best to unite them under the name *Rhodochorton*.

The question of the proper generic designation is further complicated by the fact that the older name *Audouinella* of Bory also applies to a species of this complex, *Conferva Hermanni* Roth, which is a fresh-water *Achrochaetium*-like plant.

Audouinella has not received general recognition, but has been regarded as synonymous with *Chantransia* De Candolle (*in* Lamarck and De Candolle, 1805; 1815 ed. seen), a genus which has usually been considered as including both fresh-water and marine species; and this name was for a long time adopted, and is still used by certain investigators, in preference to *Acrochaetium* or *Audouinella*. It has been conclusively shown by Drew (1928) and others, however, that the rhodophycean representatives of *Chantransia* De Candolle were species of *Lemanea* Bory (1808) or of *Batrachospermum* Roth (1797). If the name *Chantransia* is to be applied to a genus of red algae, it would thus be either synonymous with the older *Batrachospermum* or would have to replace *Lemanea*, the retention of which as a *nomen conservandum* has, however, been sanctioned by the International Botanical Congress.

With the elimination of *Chantransia*, the name *Audouinella* gains significance, since it is the oldest generic name created for a group of plants which included a species of the *Acrochaetium* complex. When Bory (1823) proposed *Audouinella*, he placed in it the following three species: *A. funiformis*, *A. chalybaea*, and *A. miniata* [=*A. Hermanni* (Roth) Duby]. Even though *A. funiformis* is representative of *Ectocarpus* Lyngbye (1819) and *A. chalybaea* is the juvenile stage of species of *Batrachospermum* Roth (1797), the genus *Audouinella*, with the type *A. Hermanni*, is valid in accordance with Art. 51 of the International Rules of Botanical Nomenclature (1935).

If the fresh-water and marine *Acrochaetium*-like species are thus representative of the same genus, as phycologists in general, with the exception of Hamel (1925) and Smith (1933), seem to believe, the name *Audouinella* Bory (1823) would have to supplant *Acrochaetium* Nägeli (1861), or it may even have to be employed for the whole assemblage, including *Rhodochorton*, if the latter is co-generic with *Acrochaetium* as Drew (1928, 1935) and others believe.

As a preliminary step in the determination of the South African marine representatives of this assemblage, it appeared desirable to make a catalogue and an analysis of published accounts of all species of *Acrochaetium*, *Rhodochorton*, and *Audouinella*, as well as of the related genera *Colaconema* and *Kylinia*.[1] The results obtained are illuminating and seemingly go far toward a clarification of the problems concerning the limits of these genera.

It was found that if the kind of chromatophores characteristic of the type species of each of these genera is used as the chief criterion for separation, the complex resolves itself into four comparatively clear-cut genera:

1. *Rhodochorton*, whose cells contain a few to many small, discoid chromatophores.
2. *Acrochaetium*, whose cells contain one parietal or laminate chromatophore. The genera *Colaconema* Batters and *Kylinia* Rosenvinge are to be merged with *Acrochaetium*.
3. *Audouinella*, whose cells contain one or more spiral chromatophores. It includes both fresh-water and marine species. The subgenus *Grania* Rosenvinge of *Acrochaetium* becomes a synonym of *Audouinella*.
4. *Chromastrum* gen. nov., whose cells contain one or more stellate chromatophores.

The evidence in support of this arrangement follows.

When Nägeli (1861, p. 355) established *Rhodochorton*, he characterized it as consisting of branched, uncorticated, prostrate filaments which give rise to erect, uncorticated, branched axes, and reproducing by means of spores formed in cruciately divided tetrasporangia. He included two species in the genus, viz., *Conferva Rothii* Turton and *C. floridula* Dillwyn, both of which are still placed in the genus.

Acrochaetium, which Nägeli (*op. cit.*, p. 402) proposed in the same paper, was characterized as consisting of branched filaments which usually arose from a unistratose, incrusting, basal disk and usually terminated in evanescent hairs, and reproducing by means of zoöspores. He included twenty-one species in *Acrochaetium*, the majority of which are still regarded as representative of the genus, either as autonomous species or as synonyms.

According to the diagnoses of Nägeli, the primary features which distinguished these two genera thus lay in the fact that in *Rhodochorton* the branches did not end in hairs as they did in *Acrochaetium* and that *Rhodochorton* reproduced by means of tetraspores while *Acrochaetium* formed zoöspores.

In the course of time, however, it was realized not only that the sporangia of *Acrochaetium* are actually monosporangia which form immobile spores, but that certain species form tetrasporangia as well as monosporangia, while others, whose habit suggests that they belong to *Acrochaetium* rather than to *Rhodochorton*, form only tetrasporangia.

The presence or absence of hairs has likewise proved to be an undependable character, since certain species of *Acrochaetium* lack hairs while some members of *Rhodochorton* possess them.

Even though the characters relied upon by Nägeli for separation of *Rhodochorton* and *Acrochaetium* are untenable, the two genera are in general dissimilar in habit, so that phycologists have sought other criteria for segregation. It has been found by Kylin (1906), Rosenvinge (1909, pp. 82–83; 1923–1924, p. 388; 1935, p. 6), and Levring (1937, pp. 81–82) that the form and number of chromatophores offered a reasonably satisfactory basis of classification. Thus *Acrochaetium* received species whose cells contained either a parietal, a stellate, or several spiral chromatophores, while *Rhodochorton* included species whose cells possessed either a few more or less irregular, a few stellate, or many small discoid chromatophores. By this method of separation the limits of the two genera, as determined by their component species, did not alter materially though the characters relied upon were entierly different from those used by Nägeli. Furthermore, *Rhodochorton* contained species which formed only tetrasporangia as asexual reproductive organs, while in *Acrochaetium* the sporangia were of several kinds: mono-, bi-, tetra-, or polysporangia.

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[1] Two recent papers containing descriptions of new species of *Acrochaetium* were not available for consideration. They are the report by Baardseth on the algae of the Norwegian expedition to the Island of Tristan da Cunha and that by Levring on Skottsberg's algae of the Juan Fernandez Islands.

Although generally applicable, this method of separation is not without fault, since there are certain intermediate types, such as *Rhodochorton floridulum* (with four stellate chromatophores) and *R. membranaceum* (with several ribbon-like chromatophores), which, on the basis of the chromatophores, may justifiably be assigned to either genus. It is primarily such species as *R. floridulum* which induced Drew to merge the two genera.

As has been mentioned, Nägeli included in *Rhodochorton* two species: *R. Rothii*, whose cells have many small, discoid chromatophores, and *R. floridulum*, whose cells contain four stellate chromatophores. *R. Rothii*, which is the first species listed by Nägeli, was designated as the type of the genus by Schmitz in 1889. Our concept of *Rhodochorton* must thus be based primarily on this plant; and if only species with similar chromatophores are placed in this genus, it becomes a comparatively well-defined unit. Of the species currently assigned to *Rhodochorton*, *R. floridulum* is to be removed to *Chromastrum* gen. nov. and *R. membranaceum* is to be transferred to *Audouinella*. The similarity in the form of the chromatophores of the latter species to those of *Acrochaetium efflorescens*, which is representative of the subgenus *Grania* of Rosenvinge (1909), or *Audouinella* in the sense of the present article, has previously been remarked upon by Rosenvinge (1935, p. 6). *Rhodochorton repens* Jónsson is to be transferred to *Acrochaetium*, where it becomes *A. Jónssonii* nom. nov.; while *R. velutinum* (Hauck) Hamel is synonymous with *Acrochaetium minutissimum* (Zanard.) Näg., and *R. speluncarum* Collins and Hervey has been shown by Howe (1920) to be a species of *Spermothamnion*.

It may be pointed out here that although the plant described and figured by Nägeli as *Rhodochorton Rothii* is representative of this genus as understood by Nägeli and subsequent writers, the specific epithet *Rothii* is misapplied, since it is based on *Conferva Rothii* Turton, which is another name for *Ceramium violaceum* Roth. This plant of Roth is not representative of *Rhodochorton*, but is a species of *Polysiphonia*. A full discussion of this nomenclatural confusion is given under *Rhodochorton purpureum*.

Sexual organs have thus far been observed only in *Rhodochorton penicilliforme*, whose spermatangia have been described and figured by Rosenvinge (1923–1924). The apparent absence of sexual plants in so widely distributed and well-known a species as *R. Rothii* suggests that sexuality may have been lost in this, and possibly other, species of the genus, and that tetraspore formation is not associated with meiosis. Such a condition is not without precedent in the red algae, for it has been shown by Svedelius (1937) that in *Lomentaria rosea,* which in European waters lacks sexual plants, tetraspore formation is not preceded by a reduction division. The possibility that certain species of *Rhodochorton* merely represent phases in the life cycle of other algae should also not be entirely excluded even though at present there is no evidence in support of it.

Owing to the lack of knowledge concerning the female reproductive organs, it has not been possible to determine the systematic position of *Rhodochorton.* Some writers have placed it as a genus of uncertain affiliation in the Ceramiaceae, while others have assigned it to the Nemalionales. Miranda (1932) is inclined to refer it to the Cryptonemiales on account of the similarity of the juvenile stages of *R. penicilliforme* to those of certain members of this order. In habit, however, *Rhodochorton* bears no resemblance to any of the Cryptonemiales, and its chromatophores are not of the type characteristic of the Nemalionales. None of its known features, however, would cause it to be excluded from the Ceramiaceae; and it seems best to retain it in this family as a *genus inserte sedis.*

Acrochaetium as understood by the majority of writers is composed of species whose cells contain either a single parietal or laminate chromatophore, one to a few spiral chromatophores, or a single stellate chromatophore. In regard to the form of this organelle, *Acrochaetium* thus embraces a heterogeneous assortment of species which may properly be segregated into three genera. That a separation on this basis is in accordance with natural kinships and differences seems likely from comparison with other groups of algae. Thus, to cite but one example, the type of chromatophore has been found to be a reliable indicator of relationships in the separation of such closely related genera of green algae as *Mougeotia* (with a laminate chromatophore), *Spirogyra* (with one or more spiral chromatophores), and *Zygnema* (with stellate chromatophores).

When Nägeli (1861) established *Acrochaetium* he made no mention of the chromatophores. Moreover, the species which he assigned to it show one or the other of all three types. The kind of chromatophore typical of *Acrochaetium* in the narrow sense may, however, be determined from *A. Daviesii,* which is both the first species listed by Nägeli and the one which Drew (1928, p. 147) by implication has designated as lectotype of the genus. This species possesses a parietal chromatophore. Happily, a large majority of the 160-odd species of *Acrochaetium* in the broad sense show this type of chromatophore. In rare instances, the primarily single chromatophore becomes divided into a few smaller ones (cf. Drew, 1928, p. 156), but the number of chromatophores never approaches that characteristic of *Rhodochorton Rothii* (cf. Taylor, 1937, pl. 45, fig. 2).

In 1906 (p. 122) Kylin remarked that on the basis of their spiral chromatophores it might be justifiable to erect a new genus for the marine *Acrochaetium efflorescens* and *A. pectinatum;* and Rosenvinge in 1909 (p. 134), acting upon this suggestion, created for these species the subgeneric category *Grania.*

It would thus seem logical to elevate *Grania* to the status of genus. However, in form of chromatophore *Acrochaetium efflorescens* and *A. pectinatum* agree so closely with the fresh-water species (cf. Skuja, 1934, pp. 175–177; Drew, 1935, p. 448), for which the generic name *Audouinella* Bory (1823) is available, that it seems best to regard all species with spiral chromatophores as representative of the same genus. In addition to *Acrochaetium efflorescens* and *A. pectinatum, Rhodochorton mem-*

branaceum is the only other marine species which at present, and in accordance with the same criterion, seems to be referable to *Audouinella.*

Since there is no earlier generic name for the species with stellate chromatophores, it becomes necessary to propose a new one. The name *Chromastrum* is suggested. In addition to some thirty-three species of *Acrochaetium*, *Rhodochorton floridulum*, whose cells contain four stellate chromatophores, is to be referred to *Chromastrum.*

Acrochaetium, *Audouinella*, and *Chromastrum* are closely related members of the Nemalionales, within which they constitute a natural family to which the name Chantransiaceae was given by Kylin in 1928. However, this name is in contravention of Art. 23 of the International Rules of Botanical Nomenclature (1935), since the genus *Chantransia* De Candolle did not include a single representative of this group of algae. The family was recently rechristened Acrochaetiaceae by Fritsch (1944, p. 258, note).

As representative examples of species of these genera in which the development of the gonimoblast has been studied, the following may be cited:

Acrochaetium: A. Bornetii nom. nov (Bornet and Thuret, 1876; Kylin, 1930, both as *Chantransia corymbifera*).

Audouinella: A. efflorescens (Kylin, 1906; Rosenvinge, 1909, both as *Chantransia efflorescens*) and *A. violacea* (Drew, 1935, as *Rhodochorton violaceum*).

Chromastrum: C. rhipidandrum (Rosenvinge, 1909; Kylin, 1928, both as *Chantransia rhipidandra*).

In agreement with the majority of other Nemalionales, *Acrochaetium* and *Chromastrum* are, as far as is known, composed of species that are haplobiontic. *Audouinella*, on the other hand, includes, in addition to several haplobiontic species, two that are diplobiontic. One of them, *A. efflorescens*, is a marine, and the other, *A. violacea*, a fresh-water species. In the latter both the sexual and asexual generations propagate themselves by means of monospores (Drew, 1935). Monosporangia are also formed in *A. efflorescens*, but it has not yet been determined whether they are formed by the sexual, the asexual, or both generations.

Since the phenomenon of an alternation of generations is so rarely shown by members of the Nemalionales, its occurrence in so simple a genus as *Audouinella* is of much phylogenetic interest. The only other Nemalionales which are known to have a similar life cycle are the highly evolved genera *Galaxaura* and *Actinotrichia* (Svedelius, 1944). *Audouinella efflorescens* and *A. violacea* have a life cycle which involves a seasonal as well as morphological alternation of generations. These cycles have been discussed by Rosenvinge (1909, p. 137) and Svedelius (1915, pp. 48–50) with reference to *A. efflorescens*, and by Drew (1935, pp. 448–449) and Levring (1940, p. 81) with reference to both species.

Although *Audouinella efflorescens* and *A. violacea* are the only members of the Acrochaetiaceae which have been shown to have an alternation of generations, several other species in all three genera of this family are known to form tetrasporangia; and since these organs are characteristic of the diploid condition, it may be assumed that the plants producing them are diploid. Certain of the tetrasporangium-forming species also reproduce by means of monosporangia, which serve the purpose of accessory reproductive organs, but, in addition to *Audouinella efflorescens* and *A. violacea*, *Acrochaetium botryocarpum* is the only supposedly tetrasporangium-forming species which forms sexual organs. There is no direct evidence concerning the role of the tetrasporangia in the life cycle of the nonsexual species, but a comparison with other red algae suggests two alternatives. In certain instances these so-called species may be merely the tetrasporic generation of other supposedly haplobiontic sexual species. Such a relationship has already been shown by Kylin (1906) to exist between at least one pair of "species." He established that the tetrasporic *Rhodochorton chantransioides* was but the asexual generation of *Audouinella efflorescens* (*Chantransia efflorescens*). In other species meiosis may have become permanently suppressed, as in *Lomentaria rosea*, which has already been referred to, with the result that the diploid asexual generation is the only one in the life cycle.

In the majority of Acrochaetiaceae, monosporangia are the only known organs of reproduction, while in a small number of species sexual as well as asexual organs are formed. It seems probable that in the greater portion of monosporic species there is no method of reproduction other than by monospores. In such forms sexuality may not as yet have developed, or it may have been lost.

In the course of this study, attention was directed to the genera *Colaconema* and *Kylinia*, which in many ways are very similar to *Acrochaetium*. It is concluded that these genera should be merged with *Acrochaetium*.

Colaconema was erected by Batters in 1896 on the basis of the cuplike nature of the cell supporting the monosporangium. He included three species—all new—in this genus, viz., *C. Bonnemaisoniae*, *C. Chylocladiae*, and *C. ? reticulatum*. Of these, only the first two need be considered in connection with the validity of the genus, since they were the only ones in which sporangia were observed. With reference to *C. Chylocladiae* Batters remarked, however, that the cuplike shape of the stalk cell was not conspicuous, and in 1902 he removed this species to *Acrochaetium*. *C. Bonnemaisoniae* thus remained as the only species which showed the character upon which the genus was established, and hence is to be regarded as the type of *Colaconema*. In 1937 Levring showed that this species in reality belongs to *Acrochaetium*, or *Chantransia* as he called it, and his conclusions have been confirmed by Feldmann (1939), who made the combination *Acrochaetium Bonnemaisoniae*.

With the removal of the type species to *Acrochaetium* there remains no alternative but to relegate *Colaconema* to the synonymy of *Acrochaetium*. According to Levring (*op. cit.*, p. 94) and Feldmann (*op. cit.*, p. 458), *C. Bonnemaisoniae* has a parietal chromatophore, which shows moreover that *Colaconema* should be considered synonymous with *Acrochaetium* in the narrow sense. In addition to *C. ? reticulatum* Batters, the following species which have been credited to *Colaconema* are to be transferred to *Acrochaetium: C. americana* Jao (1936), *C. Asperagopsis* Chemin (1926), and *C. simplex* Inagaki (1935), which becomes *Acrochaetium japonicum* nom. nov.

The genus *Kylinia* was established by Rosenvinge in 1909 to receive a new species, *K. rosulata*, which bore a great resemblance to *Acrochaetium parvulum* but, according to Rosenvinge (*op. cit.*, p. 143), differed from it in that the spermatangia were borne upon "... peculiar narrow, cylindrical, colourless cells" which he termed androphores. Levring (1935*a*, p. 41) has also remarked upon the close resemblance which *K. rosulata* bears to species of *Acrochaetium*, especially *A. parvulum;* but his material did not show spermatangia. The feature whereby *Kylinia* is separated from *Acrochaetium* is so insignificant, however, that it seems best to unite it with the latter. Kylin (1928, p. 8) has apparently arrived at the same conclusion, for he cited amongst others *K. rosulata* as a species of *Chantransia* which shows sexual reproduction. In addition to *K. rosulata,* one other species, *K. scapae* Lyle (1929, p. 245), has been credited to *Kylinia.* This species should likewise be transferred to *Acrochaetium.* According to both Rosenvinge and Levring, *K. rosulata* seems to have a parietal chromatophore, which indicates that *Kylinia* is synonymous with *Acrochaetium* in the narrow sense.

According as the plants are attached to the external surface of the host or live partly to wholly within it, and on the basis of the basal structure of the thalli, *Acrochaetium* has been divided into three main groups, as follows:

Group I. Frond epiphytic or epizoic, with a single basal cell.

Group II. Frond epiphytic or epizoic, with a multicellular basal layer.

Group III. Frond partly to almost wholly endophytic or endozoic.

This method of arrangement has proved very useful (cf. Rosenvinge, 1909; Hamel, 1928*a*, 1928*b*) and is adopted in the following catalogue of species of *Acrochaetium* and *Chromastrum. C. floridulum* lives on sand-covered rocks, but has a creeping base and is consequently included in Group II. In certain instances the method of attachment is unknown; following Hamel (1928*b*), such species will be placed in a separate group.

Acrochaetium Näg.

Nägeli, Morph. u. Syst. Ceram.: 402, 1861. *Chantransia,* various authors (in part, not of De Candolle). *Rhodochorton,* various authors (in part). *Colaconema* Batters, Some new Br. mar. alg.: 8, 1896. *Kylinia* Rosenvinge, Mar. alg. Denmark 1 (1): 141, 1909.

Plants microscopic, composed of branched, uniseriate filaments which frequently end in hairs and which are attached to the surface of the host by a single holdfast cell or a multicellular basal layer, or which are partly to almost wholly imbedded in the tissues of the host. Cells of the filaments containing a single parietal or laminate chromatophore, which in a few species divides into several, and a single or rarely a few pyrenoids or, in certain species, apparently none.

Asexual reproduction usually by monospores but at times by bi-, tetra-, or polyspores.

Sexual reproduction infrequent, monoecious or dioecious. Spermatangia usually occurring in small clusters at the tips of lateral branchlets, occasionally directly on the main filaments, in monoecious species at times directly on the carpogonium, and in *A. rosulatum* at the ends of special narrow cells. Carpogonia borne laterally on erect branches, usually sessile but occasionally on a one-celled stalk. Gonimoblast springing directly from the carpogonium and forming solitary carposporangia at the ends of its branches.

Type species: *Acrochaetium Daviesii* (Dillw.) Näg.

The species which in the following list are marked with an asterisk are provisionally left in *Acrochaetium,* though the structure of the chromatophore is not known.

Reproduction is asexual and by monospores only unless otherwise stated.

GROUP I. Frond epiphytic or epizoic, with a single basal cell.

Asexual reproduction in all known species by monospores only.

1. *Acrochaetium affine* Howe et Hoyt, *in* Mem. New York Bot. Gard. 6: 118, pl. 15, 1916; Hoyt, Mar. alg. Beaufort: 471, pl. 119, 1920.

Remarks: Reproduction sexual as well as asexual.

Geogr. distr.: North Carolina on *Dictyota, Spyridia,* and other hosts.

*2. *Acrochaetium bahreinii* Børgesen, Mar. alg. Iranian Gulf: 102, fig. 26, 1939.

Geogr. distr.: Iranian Gulf on *Dictyota.*

*3. *Acrochaetium Battersianum* Hamel, *in* Rev. Alg. 3: 177, 1928; Newton, Br. seaweeds: 253, 1931. *Chantransia microscopica* Foslie, Batters, *in* Jour. Bot. 34: 9, 1896.

Remarks: Reproduction sexual as well as asexual.
Geogr. distr.: England on *Porphyra.*

*4. *Acrochaetium caesareae* Feldmann, *in* Bul. Soc. Hist. Nat. Afr. Nord 22: 223, fig. 5, 1931.

Geogr. distr.: Mediterranean on *Porphyra.*

5. *Acrochaetium catenulatum* Howe, Mar. alg. Peru: 84, pl. 31, figs. 12–18, 1914; Kylin, *in* Kylin und Skottsberg, Subantark. u. antark. Meeresalg. 2: 3, fig. 1, 1919. *Rhodochorton catenulatum* (Howe) Nakamura, Rhodochorton from Japan 1: 273, fig. 1, 1941.

Geogr. distr.: Tierra del Fuego on *Ceramium,* Peru on *Chaetomorpha,* East Indies on *Chaetomorpha* and *Chondria,* Japan on *Sphacelaria.*

*6. *Acrochaetium Dufourii* (Collins) Børgesen, Mar. alg. Danish W. Ind. 3 (1): 19, 1915; Hoyt, Mar. alg. Beaufort: 470, fig. 26, 1920; Collins, *in* Phyc. Bor.-Am., fasc. 32: No. 1594, 1909 (*nomen nudum*). *Chantransia Dufourii* Collins, *in* Rhodora 13: 187, 1911.

Geogr. distr.: North Carolina on *Sargassum,* Bermuda on *Dictyota.*

7. *Acrochaetium dwarkense* Børgesen, *in* Kew Bull. 1932: 114, fig. 2, 1932.

Geogr. distr.: India on Dictyotaceae.

8. **Acrochaetium Eastwoodae** (Setch. et Gardn.) Papenfuss, comb. nov. *Rhodochorton Eastwoodae* Setchell et Gardner, Mar. alg. Revillagigedo Isls. Exped.: 166, pl. 4, fig. 8, 1930.

Geogr. distr.: Revillagigedo Islands on *Dictyota.*

9. *Acrochaetium erectum* Børgesen, *in* Kew Bull. 1932: 114, fig. 1, 1932.

Geogr. distr.: India on *Agardhiella.*

10. *Acrochaetium gynandrum* (Rosenv.) Hamel, *in* Rev. Alg. 3: 107, 176, fig. 15, 1928. *Chantransia gynandra* Rosenvinge, Mar. alg. Denmark 1 (1): 88, fig. 18, 1909.

Remarks: Reproduction sexual as well as asexual.
Geogr. distr.: Denmark and Atlantic coast of France on *Ectocarpus.*

*11. **Acrochaetium Hancockii** (Dawson) Papenfuss, comb. nov. *Rhodochorton Hancockii* Dawson, Mar. alg. Gulf Calif.: 255, pl. 41, figs. 4–6, 1944.

Geogr. distr.: Gulf of California on *Gelidium.*

*12. *Acrochaetium Hoytii* Collins, *in* Rhodora 10: 134, 1908; Hoyt, Mar. alg. Beaufort: 470, figs. 27–28, 1920.

Remarks: Reproduction sexual as well as asexual.
Geogr. distr.: North Carolina on *Dictyota.*

13. *Acrochaetium microfilum* Jao, *in* Bull. Torrey Bot. Club 63: 240, pl. 10, figs. 1–5, 1936; Taylor, Mar. alg. n.-east. N. Am.: 232, pl. 32, figs. 1–5, 1937.

Geogr. distr.: New England on *Polysiphonia.*

14. **Acrochaetium rosulatum** (Rosenv.) Papenfuss, comb. nov. *Kylinia rosulata* Rosenvinge, Mar. alg. Denmark 1 (1): 141, fig. 67, 1909; Distr. Rhodophyc. Dan. waters: 8, 1935; Levring, Algenfl. Kullen: 41, fig. 8 f–m, 1935.

Remarks: Reproduction sexual as well as asexual.
Geogr. distr.: North Sea and Baltic on various algae.

15. **Acrochaetium ryukyuense** (Nakam.) Papenfuss, comb. nov. *Rhodochorton ryukyuense* Nakamura, Rhodochorton from Japan 1: 275, figs. 2–3, 1941.

Remarks: Reproduction sexual as well as asexual.
Geogr. distr.: Japan on *Sphacelaria* and *Galaxaura.*

16. *Acrochaetium Sargassi* Børgesen, Mar. alg., Danish W. Ind. 3 (1): 17, figs. 7–10, 1915; Taylor, Mar. alg. Florida: 134, pl. 22, figs. 1–5, 1928.

Remarks: Reproduction sexual as well as asexual.
Geogr. distr.: Virgin Islands on *Sargassum,* Florida on various algae, especially *Padina* and *Pocockiella,* East Indies on *Sargassum.*

*17. **Acrochaetium scapae** (Lyle) Papenfuss, comb. nov. *Kylinia scapae* Lyle, *in* Jour. Linn. Soc. London, Botany 48: 245, figs. 6–7, 1929.

Geogr. distr.: Scapa Flow on *Cladophora.*

18. **Acrochaetium simplex** (Drew) Papenfuss, comb. nov. *Rhodochorton simplex* Drew, Chantransia, Rhodochorton, and Acrochaetium: 165, pl. 37, figs. 4–11, 1928.

Remarks: Reproduction sexual as well as asexual.
Geogr. distr.: California on *Ectocarpus.*

19. *Acrochaetium Spathoglossi* Børgesen, *in* Jour. Indian Bot. Soc. 16: 30, fig. 14, 1937.

Geogr. distr.: India on *Spathoglossum.*

*20. *Acrochaetium subpinnatum* Bornet ex Hamel, *in* Rev. Alg. 3: 113, 175, fig. 17, 1928.

Geogr. distr.: Mediterranean on *Chaetomorpha.*

*21. *Acrochaetium trifilum* (Buff.) Batters, Cat. Br. mar. alg.: 58, 1902; Hamel, *in* Rev. Alg. 3: 106, fig. 14 a–d, 1928. *Chantransia trifila* Buffham, *in* Jour. Quekett Micr. Club, Ser. 2, 5: 25, pl. 3, figs. 1–4, 1892.

Geogr. distr.: England and Atlantic coast of France on *Cladophora,* Mediterranean on *Chromastrum virgatulum,* Adriatic on *Chaetomorpha.*

*22. *Acrochaetium unilaterale* (Kjellm.) Hamel, *in* Rev. Alg. 3: 178, 1928. *Chantransia unilateralis* Kjellman, *in* Arkiv. Bot. 5 (14): 11, pl. 2, figs. 1–4, 1906.

Geogr. distr.: Island of Jan Mayen (Arctic) on *Halosaccion.*

23. **Acrochaetium Zosterae** Papenfuss, nom. nov. *Acrochaetium subseriatum* Jao, *in* Bull. Torrey Bot. Club 63: 243, pl. 11, figs. 5–7, 1936; Taylor, Mar. alg. n.-east. N. Am.: 232, pl. 33, figs. 5–7, 1937 (not of Børgesen, 1932).

Geogr. distr.: New England on *Zostera.*

Group II. Frond epiphytic or epizoic, with a multicellular basal layer. *Acrochaetium Thuretii* is the only species of this group which is known to show sexual reproduction.

24. *Acrochaetium attenuatum* (Rosenv.) Hamel, *in* Rev. Alg. 3: 192, 1928; Jao, *in* Bull. Torrey Bot. Club 63: 244, pl. 12, fig. 1, 1936. *Chantransia attenuata* Rosenvinge, Mar. alg. Denmark 1 (1): 106, fig. 35, 1909.

Geogr. distr.: North Atlantic on *Polysiphonia* and *Desmarestia.*

25. *Acrochaetium caespitiforme* Børgesen, Mar. alg. Danish W. Ind. 3 (6): 446, fig. 416, 1920.

Geogr. distr.: Virgin Islands on *Padina.*

*26. *Acrochaetium caespitosum* (J. Ag.) Näg., Hamel, *in* Rev. Alg. 3: 136, 194, fig. 33, 1928 (excl. syn. *Chantransia Lorrain-Smithiae* Lyle).

Remarks: Asexual reproduction by mono-, bi-, or tetraspores.
Geogr. distr.: Atlantic coast of France on *Patella.*

27. *Acrochaetium canariense* Børgesen, Mar. alg. Canary Isls. 3 (1): 17, figs. 9–11, 1927.

Remarks: Asexual reproduction by mono-, bi, or tetraspores. Tetrasporangia cruciately, irregularly, or seriately divided.
Geogr. distr.: Canary Islands on *Gelidium.*

28. *Acrochaetium clandestinum* (Mont.) Howe, Mar. alg. Peru: 86, pl. 31, figs. 19–24, 1914.

Geogr. distr.: Peru on *Chaetomorpha* and *Cladophora.*

29. *Acrochaetium Cymopoliae* Børgesen, Mar. alg. Canary Isls. 3 (1): 22, fig. 12, 1927.

Geogr. distr.: Canary Islands on *Cymopolia.*

*30. *Acrochaetium Dasyae* Collins, *in* Rhodora 8: 191, 1906; Hamel, *in* Rev. Alg. 3: 171, 189, fig. 47 b–g, 1928; Taylor, Mar. alg. n.-east. N. Am.: 231, 1937.

Geogr. distr.: New England on *Dasya.*

31. *Acrochaetium Daviesii* (Dillw.) Nägeli, Beitr. Morph. u. Syst. Ceram.: 405, figs. 26–27, 1861; Hamel, *in* Rev. Alg. 3: 133, 192, fig. 31, 1928; Børgesen, Mar. alg. Canary Isls. 3 (1): 25, fig. 15, 1927; Taylor, Mar. alg. n.-east. N. Am.: 234, pl. 31, figs. 8–10, 1937. *Chantransia Daviesii* (Dillw.) Thur., Rosenvinge, Mar. alg. Denmark 1 (1): 104, fig. 34, 1909.

Remarks: Asexual reproduction by tetraspores as well as monospores.
Geogr. distr.: North Atlantic on various algae, Mediterranean on *Posidonia,* Pacific coast of North America on various algae.

32. **Acrochaetium densum** (Drew) Papenfuss, comb. nov. *Rhodochorton densum* Drew, Chantransia, Rhodochorton, and Acrochaetium: 168, pl. 38, figs. 17–24, 1928.

Geogr. distr.: California on *Spongomorpha.*

33. *Acrochaetium Desmarestiae* Kylin, Mar. red alg. Friday Harbor: 10, fig. 4 a–f, 1925. *Rhodochorton Desmarestiae* (Kylin) Drew, Chantransia, Rhodochorton and Acrochaetium: 168, pl. 38, fig. 16, 1928.

Geogr. distr.: Pacific coast of North America on *Desmarestia.*

34. *Acrochaetium discoideum* Børgesen, Mar. alg. Easter Isl.: 271, fig. 17 b–d, 1920.

Geogr. distr.: Easter Island on *Sargassum.*

35. *Acrochaetium flexuosum* Vickers, Børgesen, Mar. alg. Danish W. Ind. 3 (1): 34, figs. 29–30, 1915; Hamel, *in* Rev. Alg. 3: 171, 193, fig. 47 a, 1928; Taylor, Mar. alg. n.-east. N. Am.: 233, 1937.

Geogr. distr.: West Indies on *Chaetomorpha,* New England on coarse filamentous algae, East Indies on *Chondria* and *Chaetomorpha.*

*36. *Acrochaetium fuegiense* Kylin, *in* Kylin und Skottsberg, Subantark. u. antark. Meeresalg. 2. Rhodophyc.: 5, fig. 3, 1919.

Geogr. distr.: Tierra del Fuego and Falkland Islands on *Ceramium.*

37. *Acrochaetium globosum* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 28, figs. 21–22, 1915.

Geogr. distr.: Virgin Islands on *Chaetomorpha.*

38. *Acrochaetium gracile* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 26, figs. 19–20, 1915.

Geogr. distr.: Virgin Islands on *Sargassum* and Canary Islands on *Gelidium.*

39. *Acrochaetium Iyengarii* Børgesen, *in* Kew Bull. 1933: 113, fig. 1, 1933.

Geogr. distr.: India on *Chaetomorpha.*

40. **Acrochaetium Jónssonii** Papenfuss, nom. nov. *Rhodochorton repens* Jónsson, Mar. alg. Iceland 1: 147, fig. 4, 1901 (not *Acrochaetium repens* Børgesen, 1915).

Remarks: Asexual reproduction by tetraspores.
Geogr. distr.: Iceland on *Alaria.*

*41. *Acrochaetium krusadii* Børgesen, *in* Jour. Indian Bot. Soc. 16: 32, figs. 17–19, 1937.

Geogr. distr.: Southern India on *Dictyota.*

*42. *Acrochaetium Lenormandi* (Suhr ex Kütz.) Näg., Hamel, *in* Rev. Alg. 3: 138, 191, fig. 34, 1928.

Geogr. distr.: Cherbourg on *Chaetomorpha.*

43. *Acrochaetium Leptonema* (Rosenv.) Børgesen, Mar. alg. Danish W. Ind. 3 (1): 31, 1915; Hamel, *in* Rev. Alg. 3: 129, fig. 29, 1928. *Chantransia leptonema* Rosenvinge, Mar. alg. Denmark 1 (1): 118, figs. 46–48, 1909; Levring, Algenfl. Kullen: 38, fig. 7 a–e, 1935; Algenveg. Blekinge: 80, fig. 23 c–f, 1940.

Geogr. distr.: North Sea and Baltic on various algae, Mediterranean on *Posidonia,* Bermuda on *Dictyopteris,* Dry Tortugas (host not indicated).

*44. *Acrochaetium Lorrain-Smithiae* (Lyle) Newton, Br. seaweeds: 256, 1931. *Chantransia Lorrain-Smithiae* Lyle, Mar. alg. Guernsey: 13, fig. 1, 1920.

Remarks: Hamel (1928*b*, p. 191) regards this species as synonymous with *A. caespitosum,* but Newton (*loc. cit.*) retains it as an independent entity.
Geogr. distr.: England on *Saccorhiza.*

*45. *Acrochaetium mahumetanum* Hamel, *in* Rev. Alg. 3: 128, 189, fig. 28, 1928.

Remarks: Asexual reproduction by bispores as well as monospores.
Geogr. distr.: Algiers on *Chaetomorpha* and *Ectocarpus.*

*46. *Acrochaetium minutissimum* (Zanard.) Nägeli, Morph. u. Syst. Ceram.: 405, 1861 (only as to binomial); Thuret ex Bornet, *in* Bornet, Acrochaetium et Chantransia: XXII, 1904 (only as to binomial). *Callithamnion minutissimum* Zanardini, Syn. alg. Adriat.: 176, pl. 2, fig. 3, 1842 (not of Kützing, 1843). *Rhodochorton velutinum* (Hauck) Hamel, *in* Rev. Alg. 3: 155, 201, fig. 40 e–k, 1928 (excl. syns. *Callithamnion sparsum* and *Acrochaetium sparsum*).

Remarks: Hamel (1928*a*, p. 156; 1928*b*, p. 201) has reduced this species to the synonymy of *Rhodochorton velutinum;* but since the specific epithet *minutissimum* is the older, and since the plant seems to be a species of *Acrochaetium* rather than of *Rhodochorton,* it is necessary to retain the name *A. minutissimum.* Hamel also includes the *Callithamnion sparsum* of Harvey (*in* Hooker, 1833, p. 348) in the synonymy of *R. velutinum,* but according to Batters (1896*a*, p. 390) *C. sparsum* forms monospores. This indicates that *C. sparsum* should be excluded from *Rhodochorton;* also that it is not synonymous with *Acrochaetium minutissimum* (or *R. velutinum*), which, according to Hamel (1928*a*, p. 156) forms bispores as well as monospores.

Geogr. distr.: Adriatic and Mediterranean on *Cystoseira.*

47. *Acrochaetium minutum* (Suhr) Hamel, *in* Rev. Alg. 3: 143, 163, 194, 1928. *Callithamnion minutum* Suhr, *in* Flora 14: 727, 1831. *Rhodochorton minutum* (Suhr) Reinke, Atlas deutsch. Meeresalg., heft 2: 59, pl. 40, 1892. *Callithamnion minutissimum* Kütz., Kützing, Tab. phyc. 11: 18, pl. 57, fig. 1, 1861 (not of Zanardini, 1842, p. 176). *Acrochaetium minutissimum* Nägeli, Morph. u. Syst. Ceram.: 405, 1861.

Remarks: Asexual reproduction by tetraspores.

Geogr. distr.: Baltic on species of *Polysiphonia.*

48. *Acrochaetium netrocarpum* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 24, figs. 17–18, 1915.

Geogr. distr.: Virgin Islands on *Caulerpa.*

49. *Acrochaetium pacificum* Kylin, Mar. red alg. Friday Harbor: 11, fig. 4 g–i, 1925. *Rhodochorton pacificum* (Kylin) Drew, Chantransia, Rhodochorton, and Acrochaetium: 169, pl. 38, fig. 25, 1928.

Geogr. distr.: Pacific coast of North America on various algae and *Sertularia.*

*50. *Acrochaetium pallens* (Zanard.) Näg., Hamel, *in* Rev. Alg. 3: 142, 194, 1928.

Remarks: Asexual reproduction by tetraspores as well as monospores.

Geogr. distr.: Adriatic on larger algae.

51. *Acrochaetium plumosum* (Drew) Smith, Mar. alg. Monterey Penin.: 180, 1944. *Rhodochorton plumosum* Drew, Chantransia, Rhodochorton, and Acrochaetium: 173, pl. 39, fig. 29, 1928.

Geogr. distr.: California on various members of the Laminariales.

52. *Acrochaetium polysporum* Howe, Mar. alg. Peru: 88, pl. 31, figs. 1–11, 1914.

Remarks: Asexual reproduction by polyspores.

Geogr. distr.: Peru on *Lessonia* and *Macrocystis.*

*53. *Acrochaetium radians* Hamel, *in* Rev. Alg. 3: 168, 193, fig. 44 a–f, 1928.

Geogr. distr.: Island of Guadeloupe (host not indicated).

54. *Acrochaetium radiatum* Jao, *in* Bull. Torrey Bot. Club 63: 246, pl. 10, figs. 18–25, 1936; Taylor, Mar. alg. n.-east. N. Am.: 237, pl. 32, figs. 18–25, 1937.

Geogr. distr.: New England on *Polysiphonia.*

55. *Acrochaetium reductum* (Rosenv.) Hamel, *in* Rev. Alg.: 3, 189, 1928. *Chantransia reducta* Rosenvinge, Mar. alg. Denmark 1 (1): 120, fig. 49, 1909; Levring, Algenfl. norw. Westküste: 89, 1937.

Geogr. distr.: Denmark, Sweden, Norway on *Polysiphonia* and *Rhodomela.*

*56. *Acrochaetium Sagraeanum* (Mont.) Bornet, Acrocheatium et Chantransia: XXI, 1904; Collins and Hervey, Alg. Bermuda: 97, 1917; Hamel, *in* Rev. Alg. 3: 171, 193, fig. 46, 1928.

Geogr. distr.: West Indies and Bermuda on *Zostera, Stypopodium,* and *Dictyopteris;* New England on *Ruppia.*

57. *Acrochaetium sancti-thomae* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 30, figs. 23–24, 1915. *Rhodochorton sancti-thomae* (Børg.) Nakamura, Rhodochorton from Japan 1: 280, figs. 5–7, 1941.

Geogr. distr.: Virgin Islands on *Sargassum,* Japan on *Ecklonia.*

*58. *Acrochaetium Savianum* (Menegh.) Näg., Hamel, *in* Rev. Alg. 3: 135, 192, fig. 32, 1928.

Geogr. distr.: Genoa on *Zostera.*

*59. *Acrochaetium seiriolanum* (Harvey-Gibson) Rosenvinge, Mar. alg. Denmark 3 (3): 390, 1923–1924. *Rhodochorton seiriolanum* Harvey-Gibson, *in* Proc. Linn. Soc. London, Botany 28: 204, pl. 34, figs. 1–5, 1891; Børgesen, Mar. alg. Faeröes: 396, 1902.

Remarks: Asexual reproduction by tetraspores.
Geogr. distr.: England on *Polysiphonia* and other algae, Faroe Islands on *Ceramium.*

60. *Acrochaetium seriatum* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 32, figs. 25–28, 1915.

Geogr. distr.: Virgin Islands on various algae and East Indies on *Posidonia.*

61. *Acrochaetium strictum* (Rosenv.) Hamel, *in* Rev. Alg. 3: 195, 1928. *Chantransia stricta* Rosenvinge, Mar. alg. Denmark 1 (1): 108, fig. 36, 1909; Levring, Algenfl. Kullen: 36, 1935.

Geogr. distr.: Denmark on *Polysiphonia,* west coast of Sweden on *Polysiphonia* and *Ceramium,* and west coast of Norway on *Cystoclonium.*

62. *Acrochaetium subseriatum* Børgesen, *in* Kew Bull. 1932: 118, figs. 6–7, 1932.

Geogr. distr.: India on *Chondria.*

63. *Acrochaetium Thuretii* (Born.) Collins and Hervey, Alg. Bermuda: 97, 1917; Hamel, *in* Rev. Alg. 3: 131, 191, fig. 30, 1928. *Chantransia Thuretii* (Born.) Kylin, Algenfl. schwed. Westküste: 119, fig. 28, 1907. *Chantransia efflorescens* var. *Thuretii* Bornet, Deux Chantransia corymbifera: XVI, pl. 1, 1904.

Remarks: Reproduction sexual as well as asexual.
Geogr. distr.: North Atlantic on a variety of algae.

64. *Acrochaetium tuticorinense* Børgesen, *in* Jour. Indian Bot. Soc. 16: 30, figs. 15–16, 1937.

Geogr. distr.: India on "a sea-grass."

65. *Acrochaetium variabile* (Drew) Smith, Mar. alg. Monterey Penin.: 179, 1944. *Rhodochorton variabile* Drew, Chantransia, Rhodochorton, and Acrochaetium: 174, pl. 38, fig. 28, pl. 39, figs. 30–31, 1928.

Geogr. distr.: Pacific coast of North America on a variety of algae.

GROUP III. Frond partly to almost wholly endophytic or endozoic.

66. *Acrochaetium Alcyonidii* Jao, *in* Bull. Torrey Bot. Club 63: 245, pl. 12, figs. 2–4, 1936; Taylor, Mar. alg. n.-east. N. Am.: 234, pl. 34, figs. 2–4, 1937.

Remarks: Asexual reproduction by bispores as well as monospores.
Geogr. distr.: New England in *Alcyonidium*.

67. **Acrochaetium americanum** (Jao) Papenfuss, comb. nov. *Colaconema americana* Jao, *in* Bull. Torrey Bot. Club 63: 237, pl. 13, fig. 8, 1936; Taylor, Mar. alg. n.-east. N. Am.: 216, pl. 29, fig. 8, 1937.

Geogr. distr.: New England in *Asparagopsis*.

68. **Acrochaetium Amphiroae** (Drew) Papenfuss, comb. nov. *Rhodochorton Amphiroae* Drew, Chantransia, Rhodochorton, and Acrochaetium: 179, pl. 40, figs. 34–37, 1928.

Geogr. distr.: California in *Amphiroa*.

69. **Acrochaetium angustum** (Drew) Papenfuss, comb. nov. *Rhodochorton angustum* Drew, Chantransia, Rhodochorton, and Acrochaetium: 185, pl. 44, figs. 54–56, 1928.

Geogr. distr.: Pacific coast of North America in *Liagora*.

*70. *Acrochaetium antillarum* Taylor, Caribbean mar. alg. Hancock Exped. 1939: 78, pl. 2, figs. 3–4, 1942.

Geogr. distr.: West Indies in *Bryopsis*.

71. *Acrochaetium Arnoldii* Weber-van Bosse, Alg. Siboga 2 (1): 194, figs. 54–55, 1921.

Geogr. distr.: East Indies in *Roschera*.

72. **Acrochaetium Asparagopsis** (Chemin) Papenfuss, comb. nov. *Colaconema Asparagopsis* Chemin, *in* Compt. Rend. Acad. Sci. Paris 183: 902, figs. 1–4, 1926.

Geogr. distr.: Atlantic coast of France in *Asparagopsis*.

73. *Acrochaetium Avrainvilleae* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 48, figs. 47–49, 1915.

Geogr. distr.: Virgin Islands in *Avrainvillea*.

*74. *Acrochaetium barbadense* (Vickers) Børgesen, Mar. alg. Danish W. Ind. 3 (1): 45, 1915; Hamel, *in* Rev. Alg. 3: 164, 181, fig. 41, 1928.

Remarks: Reproduction sexual as well as asexual.
Geogr. distr.: West Indies and Bermuda in *Liagora*.

75. *Acrochaetium bisporum* (Børgs.) Børgesen, Mar. alg. Danish W. Ind. 3 (1): 43, fig. 41, 1915.

Remarks: Asexual reproduction by bispores as well as monospores.
Geogr. distr.: Virgin Islands in *Acanthophora*.

76. *Acrochaetium Bonnemaisoniae* (Batt.) J. et G. Feldmann, *in* Bull. Soc. Hist. Nat. Afr. Nord 30: 458, 1939. *Colaconema Bonnemaisoniae* Batters, *in* Jour-Bot. 34: 8, 1896; Chemin, *in* Compt. Rend. Acad. Sci. Paris 182: 1561, figs. 1–3, 1926; Newton, Br. seaweeds: 250, fig. 154, 1931. *Chantransia Bonnemaisoniae* (Batt.) Levring, Algenfl. norw. Westküste: 94, fig. 16 a–c, 1937.

Geogr. distr.: England, west coast of Norway and Atlantic coast of France in *Bonnemaisonia asparagoides*; North Africa in *B. clavata*.

77. **Acrochaetium Bornetii** Papenfuss, nom. nov. *Chantransia corymbifera* Thuret, *in* Bornet et Thuret, Notes alg. 1: 16, pl. 5, 1876; Thuret, *in* Le Jolis, Liste alg. mar. Cherbourg: 107, 1863 (in part); Bornet, Deux Chantransia corymbifera: XIV, XX, 1904; Kylin, *in* Lunds Univ. Årsskr. N. F. Avd 2, 26 (6): 5, fig. 1, 1930. *Acrochaetium corymbiferum* (Thur.) Batters, Cat. Br. mar. alg.: 59, 1902; Hamel, *in* Rev. Alg. 3: 121, 181, fig. 25, 1928; Newton, Br. seaweeds: 255, fig. 155, 1931. *Rhodochorton corymbiferum* (Thur.) Drew, Chantransia, Rhodochorton, and Acrochaetium: 183, 1928.

Remarks: As has been shown by Bornet (1904), the first description of *Chantransia corymbifera* by Thuret (1863) was based on a mixture of two entities, the one occurring on *Ceramium* and the other on *Helminthocladia.* Although the diagnosis of the "species" was based upon plants occurring on both these genera, only *Ceramium* was cited as the host. In 1876 Thuret gave a detailed description of the plant occurring on *Helminthocladia,* and it is this alga which has retained the specific name *corymbifera.* The plant which grows on *Ceramium* was described by Bornet in 1904 as a variety, var. *Thuretii,* of *Chantransia efflorescens.* This entity was subsequently elevated by Kylin (1907) to the rank of species under *Chantransia,* and in 1917 Collins and Hervey transferred it to *Acrochaetium.*

According to Art. 64 of the International Code, the epithet *corymbiferum* must be rejected since the "species" was derived from two discordant elements. The name *Bornetii* is proposed as a substitute, and the material of Thuret (1876) which occurs on *Helminthocladia Calvadosii* (Lamour.) Setch. (= *H. purpurea*) is designated as the type.

Reproduction is sexual as well as asexual.

Geogr. dist.: Northeastern Atlantic in *Helminthocladia* and *Thuretella,* Bermuda in *Dudresnaya,* North Carolina in *Dasya,* California in *Helminthocladia.*

*78. *Acrochaetium botryocarpum* (Harv.) J. Ag., Hamel, *in* Rev. Alg. 3: 165, 184, fig. 42, 1928.

Remarks: Reproduction is sexual as well as asexual. According to Harvey (1855, p. 563), this species reproduces asexually by tetraspores. If this observation is correct [which is doubtful in view of the fact that Harvey (1851) referred to the monosporangia of *A. sparsum* as tetrasporangia], it would suggest that *A. botryocarpum* shows an alternation of generations.

Geogr. distr.: Western Australia in *Scytosiphon.*

*79. *Acrochaetium Brebneri* (Batt.) Hamel, *in* Rev. Alg. 3: 185, 1928. *Rhodochorton Brebneri* Batters, *in* Jour. Bot. 35: 437, 1897.

Remarks: Asexual reproduction by tetraspores.

Geogr. distr.: England (Plymouth) in *Gloeosiphonia.*

80. *Acrochaetium bulbosum* Hamel, *in* Rev. Alg. 3: 170, 182, fig. 45, 1928.

Geogr. distr.: Chili in a species of the Ceramiaceae.

*81. *Acrochaetium Chylocladiae* (Batt.) Batters, Cat. Br. mar. alg.: 58, 1902. *Colaconema Chylocladiae* Batters, *in* Jour. Bot. 34: 8, 1896.

Geogr. distr.: England in *Gastroclonium.*

82. **Acrochaetium coccineum** (Drew) Papenfuss, comb. nov. *Rhodochorton coccineum* Drew, Chantransia, Rhodochorton, and Acrochaetium: 192, pl. 47, fig. 82, pl. 48, figs. 83–86, 1928.

Remarks: Asexual reproduction by tetraspores.

Geogr. distr.: California in *Laminaria.*

83. *Acrochaetium Codicola* Børgesen, Mar. alg. Canary Isls. 3 (1): 33, figs. 18–20, 1927.

Geogr. distr.: Canary Islands in *Codium.*

84. *Acrochaetium Codii* (Crouan) Born., Hamel, *in* Rev. Alg. 3: 124, 185, fig. 27, 1928. *Chantransia Codii* (Crouan) Levring, Algenfl. norw. Westküste: 89, fig. 13, 1937.

Geogr. distr.: Eastern North Atlantic in *Codium.*

85. *Acrochaetium comptum* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 46, figs. 44–46, 1915.

Geogr. distr.: Virgin Islands in *Liagora.*

86. *Acrochaetium Dictyotae* Collins, *in* Rhodora 8: 193, 1906. *Rhodochorton Dictyotae* (Collins) Drew, Chantransia, Rhodochorton, and Acrochaetium: 190, pl. 47, figs. 79–80, 1928.

Geogr. distr.: California in *Dictyota.*

87. **Acrochaetium elegans** (Drew) Papenfuss, comb. nov. *Rhodochorton elegans* Drew, Chantransia, Rhodochorton, and Acrochaetium: 181, pl. 41, fig. 41, pl. 43, fig. 46, 1928.

Geogr. distr.: California in *Eisenia.*

88. *Acrochaetium emergens* (Rosenv.) Web.-v. Bosse, Alg. Siboga 2 (1): 194, 1921; Hamel, *in* Rev. Alg. 3: 186, 1928; Taylor, Mar. alg. n.-east. N. Am.: 235, 1937. *Chantransia emergens* Rosenvinge, Mar. alg. Denmark 1 (1): 128, fig. 55, 1909; Levring, Algenfl. norw. Westküste: 91, fig. 14, 1937.

Geogr. distr.: North Atlantic in *Polysiphonia.*

*89. *Acrochaetium endophyticum* Batters, *in* Jour. Bot. 34: 386, 1896.

Geogr. distr.: England in *Heterosiphonia.*

90. *Acrochaetium endozoicum* (Darb.) Batters, Cat. Br. mar. alg.: 58, 1902; Hamel, *in* Rev. Alg. 3: 126, 188, 1928; Knight and Parke, Manx alg.: 78, 114, pl. 13, figs. 34, 40, 1931. *Chantransia endozoica* Darbishire, *in* Ber. deutsch. bot. Gesellsch. 17: 15, pl. 1, 1899; Levring, Algenfl. norw. Westküste: 91, 1937.

Geogr. distr.: Northeastern Atlantic in *Alcyonidium.*

*91. *Acrochaetium Hameli* Feldmann, *in* Bull. Soc. Hist. Nat. Afr. Nord 22: 224, pl. 11, 1931.

Geogr. distr.: Mediterranean in *Porphyra.*

92. *Acrochaetium hormorhizum* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 50, figs. 50–52, 1915.

Geogr. distr.: Virgin Islands in *Champia.*

93. **Acrochaetium Howei** (Yamada) Papenfuss, comb. nov. *Rhodochorton Howei* Yamada, Notes Jap. alg. 8: 127, 1938. *Rhodochorton affine* Yamada, Notes Jap. alg. 3: 114, fig. 3 a–d, 1932 [not *R. affine* (Howe) Drew, 1928, p. 151].

Remarks: Asexual reproduction by tetraspores.
Geogr. distr.: Japan in *Codium.*

94. **Acrochaetium Hyalosiphoniae** (Nakam.) Papenfuss, comb. nov. *Rhodochorton Hyalosiphoniae* Nakamura, Rhodochorton from Japan 1: 287, figs. 14–16, 1941.

Geogr. distr.: Japan in *Hyalosiphonia.*

95. *Acrochaetium Hypneae* (Børgs.) Børgesen, Mar. alg. Danish W. Ind. 3 (1): 51, figs. 53–54, 1915.

Geogr. distr.: Virgin Islands in *Hypnea,* Bermuda in *Centroceras.*

96. **Acrochaetium inclusum** (Levring) Papenfuss, comb. nov. *Chantransia inclusa* Levring, Algenfl. norw. Westküste: 96, fig. 16 d–e, 1937.

Geogr. distr.: West coast of Norway in *Dumontia*.

97. *Acrochaetium intermedium* Jao, *in* Bull. Torrey Bot. Club 63: 242, pl. 11, figs. 1–4, 1936; Taylor, Mar. alg. n.-east. N. Am.: 231, pl. 33, figs. 1–4, 1937.

Remarks: Asexual reproduction by bispores as well as monospores.
Geogr. distr.: New England in *Dasya*.

98. *Acrochaetium interpositum* (Heydr.) Børgesen, Mar. alg. Danish W. Ind. 3 (1): 57, 1915; Hamel, *in* Rev. Alg. 3: 167, 187, 1928. *Chantransia interposita* Heydrich, *in* Ber. deutsch. bot. Gesellsch. 11: 78, pl. 22, fig. 8, 1893.

Remarks: Asexual reproduction by tetraspores.
Geogr. distr.: Bay of Islands, New Zealand, in *Codium*.

*99. **Acrochaetium japonicum** Papenfuss, nom. nov. *Colaconema simplex* Inagaki, Mar. alg. new to sci.: 44, fig. 2, 1935 (not *Rhodochorton simplex* Drew, 1928, p. 165).

Geogr. distr.: Japan in *Asparagopsis*.

100. *Acrochaetium Kuckuckianum* Hamel, *in* Rev. Alg. 3: 180, 1928. *Chantransia microscopica* var. *pygmaea* Kuckuck, Mar. Algenveg. Helgoland 2: 391, fig. 15, 1897.

Remarks: Reproduction sexual; sporangia unknown.
Geogr. distr.: Helgoland in *Porphyra*.

*101. *Acrochaetium Kylinii* Hamel, *in* Rev. Alg. 3: 187, 1928. *Rhodochorton endophyticum* Kylin, Algenfl. schwed. Westküste: 188, fig. 40, 1907 (not of Batters, 1896*b*).

Geogr. distr.: West coast of Sweden in *Delesseria*.

*102. *Acrochaetium Lauterbachii* (Schm. et Heydr.) Hamel, *in* Rev. Alg. 3: 196, 1928. *Chantransia Lauterbachii* Schmitz et Heydrich, *in* Schumann und Lauterbach, Flora deutsch. Schutzgebiete Südsee: 25, 1901 (description *in* Heydrich, *in* Ber. deutsch. bot. Gesellsch. 10: 475, 1892. as *Chantransia mirabilis*).

Remarks: Reproduction is sexual as well as asexual. Heydrich (1892, p. 475) characterized this species as having undivided tetrasporangia. Material of the original collection in Herbarium University of California (No. 409024) shows monosporangia. The chromatophore seems to be parietal, but this could not be determined with certainty. It seems likely that *A. Lauterbachii* and *A. robustum* will prove to be co-specific.
Geogr. distr.: New Guinea in *Sargassum*.

*103. *Acrochaetium Liagoraefilum* Børgesen, *in* Jour. Indian Bot. Soc. 16: 35, figs. 20–21, 1937.

Geogr. distr.: India in *Liagora*.

104. *Acrochaetium Macounii* (Collins) Hamel, *in* Rev. Alg. 3: 184, 1928. *Chantransia Macounii* Collins, Mar. alg. Vancouver Isl.: 113, 1913. *Rhodochorton Macounii* (Collins) Drew, Chantransia, Rhodochorton, and Acrochaetium: 184, pl. 43, figs. 47–52, pl. 44, fig. 53, 1928.

Remarks: Reproduction sexual as well as asexual.
Geogr. distr.: Pacific coast of North America in *Haplogloia*.

105. **Acrochaetium magnificum** (Drew) Papenfuss, comb. nov. *Rhodochorton magnificum* Drew, Chantransia, Rhodochorton, and Acrochaetium: 180, pl. 41, figs. 38–40, 1928.

Geogr. distr.: California in *Pelagophycus.*

*106. *Acrochaetium minimum* Collins, *in* Rhodora 10: 133, 1908; Taylor, Mar. alg. n.-east N. Am.: 237, 1937.

Geogr. distr.: New England in *Desmarestia.*

107. *Acrochaetium multisporum* Børgesen, *in* Jour. Indian Bot. Soc. 16: 38, figs. 22–23, 1937.

Remarks: Reproduction by polyspores.
Geogr. distr.: India in *Halymenia.*

*108. *Acrochaetium Naumannii* (Asken.) Born., Hamel, *in* Rev. Alg. 3: 166, 184, fig. 43, 1928.

Geogr. distr.: Atlantic coast of North Africa in *Codium.*

109. *Acrochaetium Nemalionis* (De Not.) Born., Hamel, *in* Rev. Alg. 3: 124, 183, fig. 26 a, 1928. *Chantransia Nemalionis* (De Not.) Ard. et Straf., Rosenvinge, Mar. alg. Denmark 1 (1): 126, figs. 53–54, 1909.

Geogr. distr.: Denmark and Mediterranean in *Nemalion,* Canary Islands in *Liagora,* Bermuda in submerged branches of *Tamarix.*

110. **Acrochaetium Nitophylli** (Levring) Papenfuss, comb. nov. *Chantransia Nitophylli* Levring, Algenfl. norw. Westküste: 93, fig. 15, 1937.

Geogr. distr.: West coast of Norway in *Nitophyllum.*

111. **Acrochaetium obscurum** (Drew) Papenfuss, comb. nov. *Rhodochorton obscurum* Drew, Chantransia, Rhodochorton, and Acrochaetium: 193, pl. 48, fig. 87, 1928.

Remarks: Asexual reproduction by tetraspores.
Geogr. distr.: California in *Laminaria* and *Desmarestia.*

112. *Acrochaetium occidentale* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 44, figs. 42–43, 1915.

Remarks: Asexual reproduction by bispores as well as monospores.
Geogr. distr.: Virgin Islands and Canary Islands in *Liagora.*

113. *Acrochaetium opetigenum* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 38, figs. 35–37, 1915.

Geogr. distr.: Virgin Islands in *Dasya.*

114. **Acrochaetium penetrale** (Drew) Papenfuss, comb. nov. *Rhodochorton penetrale* Drew, Chantransia, Rhodochorton, and Acrochaetium: 187, pl. 44, figs. 57–58, pl. 45, figs. 59–60, 1928.

Geogr. distr.: California in *Sertularia.*

115. **Acrochaetium penetrans** (Levring) Papenfuss, comb. nov. *Chantransia penetrans* Levring, *in* Bot. Notiser 1935: 456, fig. 1, 1935.

Geogr. distr.: West coast of Sweden in *Alcyonidium.*

116. *Acrochaetium phacelorhizum* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 54, figs. 57–59, 1915.

Geogr. distr.: Virgin Islands in *Codium*.

117. *Acrochaetium Polyidis* (Rosenv.) Børgesen, Mar. alg. Danish W. Ind. 3 (1): 59, 1915. *Chantransia Polyidis* Rosenvinge, Mar. alg. Denmark 1 (1): 132, figs. 59–60, 1909; Levring, *in* Bot. Notiser 1935: 460, fig. 3, 1935.

Geogr. distr.: Denmark, West coasts of Sweden and Norway in *Polyides*.

*118. *Acrochaetium polyrhizum* (Harv.) J. Ag., Hamel, *in* Rev. Alg. 3: 168, 186, 1928.

Geogr. distr.: Southern Australia in *Codium*.

119. *Acrochaetium Ralfsiae* Børgesen, Mar. alg. Easter Isl.: 273, figs. 18–19, 1920.

Geogr. distr.: Easter Island in *Ralfsia*.

120. *Acrochaetium repens* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 52, figs. 55–56, 1915; *ibid.* 3 (6): 452, fig. 420, 1920.

Geogr. distr.: Virgin Islands in *Hypnea* and *Griffithsia*.

121. **Acrochaetium reticulatum** (Batt.) Papenfuss, comb. nov. *Colaconema ? reticulatum* Batters, *in* Jour. Bot. 34: 8, 1896; Chemin, *in* Compt. Rend. Acad. Sci. Paris 182: 982, figs. 1–5, 1926; Knight and Parke, Manx alg.: 77, 114, 1931.

Geogr. distr.: England and Atlantic coast of France in *Desmarestia*.

122. *Acrochaetium rhizoideum* (Drew) Smith, Mar. alg. Monterey Penin.: 180, 1944. *Rhodochorton rhizoideum* Drew, Chantransia, Rhodochorton, and Acrochaetium: 182, pl. 42, figs. 42–44, 1928.

Geogr. distr.: Pacific coast of North America in *Codium* and *Cystophyllum*.

123. *Acrochaetium robustum* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 40, figs. 38–40, 1915; *ibid.* 3 (6): 449, fig. 418, 1920. *Rhodochorton robustum* (Børg.) Nakamura, Rhodochorton from Japan 1: 284, figs. 10–13, 1941. *Acrochaetium Sargassicolum* Børgesen, *in* Kew Bull. 1932: 115, figs. 3–5, 1932.

Remarks: Reproduction sexual as well as asexual. From Heydrich's description of *Acrochaetium Lauterbachii* (*in* Ber. deutsch. bot. Gesellsch. 10: 475, 1892, as *Chantransia mirabilis*) and from an examination of a small amount of material of this plant in Herbarium University of California, it seems likely that *A. Lauterbachii* and *A. robustum* will prove to be co-specific.

Geogr. distr.: Virgin Islands and India on *Sargassum*, Japan on *Turbinaria*.

124. *Acrochaetium sanctae-mariae* (Darb.) Hamel, *in* Rev. Alg. 3: 187, 1928; Newton, Br. seaweeds: 256, 1931. *Chantransia sanctae-mariae* Darbishire, *in* Northumberland Sea Fish. Comm. Report: 41, figs. 1–2, 1910.

Geogr. distr.: England in *Himanthalia*.

125. **Acrochaetium sinicolum** (Dawson) Papenfuss, comb. nov. *Rhodochorton sinicola* Dawson, Mar. alg. Gulf. Calif.: 256, pl. 41, figs. 1–2, 1944.

Geogr. distr.: Gulf of California in *Dictyota*.

126. *Acrochaetium spongicolum* Weber-van Bosse, Alg. Siboga 2 (1): 195, figs. 56–57, 1921.

Remarks: Reproduction not known.

Geogr. distr.: East Indies in a sponge.

127. **Acrochaetium subimmersum** (Setch. et Gardn.) Papenfuss, comb. nov. *Rhodochorton subimmersum* Setchell and Gardner, Alg. n.-west. Am.: 347, pl. 17, fig. 12, 1903; Drew, Chantransia, Rhodochorton, and Acrochaetium: 191, pl. 47, fig. 81, 1928; Nakamura, Rhodochorton from Japan 1: 290, fig. 17, 1941.

Remarks: Asexual reproduction by tetraspores.

Geogr. distr.: Pacific coast of North America in *Grateloupia* and other membranaceous Rhodophyceae, Japan in *Grateloupia*.

*128. *Acrochaetium subtilissimum* (Kütz.) Hamel, *in* Rev. Alg. 3: 120, 180, fig. 24, 1928.

Remarks: Reproduction sexual as well as asexual.

Geogr. distr.: Atlantic coast of France in *Dudresnaya*, *Stilophora*, and *Ceramium*.

129. *Acrochaetium unipes* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 35, figs. 31–34, 1915.

Geogr. distr.: Virgin Islands in *Dictyota*.

130. **Acrochaetium vagum** (Drew) Papenfuss, comb. nov. *Rhodochorton vagum* Drew, Chantransia, Rhodochorton, and Acrochaetium: 188, pl. 45, figs. 61–69, 1928.

Geogr. distr.: Pacific coast of North America in *Pterosiphonia*.

*131. **Acrochaetium Vanbosseae** Papenfuss, nom. nov. *Chantransia Liagorae* Weber-van Bosse, Mar. alg. Percy Sladen Trust Exped.: 275, 1914. *Acrochaetium Liagorae* (Web.-v. Bosse) Hamel, *in* Rev. Alg. 3: 185, 1928 (not of Børgesen, 1915, p. 58).

Remarks: Reproduction sexual as well as asexual.

Geogr. distr.: Western Indian Ocean (Coetivy Reef) in *Liagora*.

GROUP IV. Method of attachment of frond unknown.

132. *Acrochaetium ernothrix* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 59, figs. 63–64, 1915.

Geogr. distr.: Virgin Islands on *Centroceras*.

133. **Acrochaetium Gymnogongri** (Drew) Papenfuss, comb. nov. *Rhodochorton Gymnogongri* Drew, Chantransia, Rhodochorton, and Acrochaetium: 175, pl. 40, fig. 32, 1928. *Acrochaetium Gymnogongri* Setchell et Gardner, *in* Collins, Holden, and Setchell, Phyc. Bor.-Am., fasc. 45: No. 2244, 1917 (*nomen nudum*).

Remarks: Asexual reproduction by tetraspores.

Geogr. distr.: California on *Gymnogongrus*.

*134. *Acrochaetium molle* (Pilg.) Hamel, *in* Rev. Alg. 3: 196, 1928. *Chantransia mollis* Pilger, Meeresalg. Kamerun: 298, figs. 8–9, 1911.

Geogr. distr.: Cameroons on *Gracilaria*.

*135. *Acrochaetium sparsum* (Harv.) Nägeli, Beitr. Morph. u. Syst. Ceram.: 405, 1861; Batters, *in* Jour. Bot. 34: 389–390, 1896; Cat. Br. mar. alg.: 58, 1902. *Callithamnion sparsum* Harvey, *in* Hooker, Eng. fl. 5: 348, 1833; Phyc. brit. 3: pl. 297, 1851.

Remarks: Some writers credit this species to Carmichael. It was, however, described by Harvey, who merely quoted Carmichael with regard to the sporangia. In the text to plate 297 of his Phycologia Britannica (vol. 3), Harvey repeated the original description which he had given in Hooker's English Flora (vol. 5, p. 348), but instead of " 'capsules obovate sessile mostly axillary' " he wrote "tetraspores 'obovate, sessile, mostly axillary.' " Farther along on the same page he remarked, however, that he had not seen the tetrasporangia. According to Batters (1896*b*, pp. 389–390), the type material is monosporic. It seems probable therefore that *Callithamnion sparsum* Harv. is not identical with *Chantransia velutina* Hauck, with which it has been synonymized by Hamel (1928*a*, p. 155; 1928*b*, p. 201). Newton (1931, p. 253) characterizes *Acrochaetium sparsum* as forming tetrasporangia, but this report is probably based upon the statement of Harvey.

Geogr. distr.: England and Ireland on *Laminaria* and *Cladophora.*

136. **Acrochaetium tenuissimum** (Collins) Papenfuss, comb. nov. *Chantransia virgatula* f. *tenuissima* Collins, *in* Collins, Holden and Setchell, Phyc. Bor.-Am., fasc. 15: No. 741, 1900. *Acrochaetium virgatulum* f. *tenuissima* (Collins) Collins, *in* Rhodora 8: 194, 1906. *Rhodochorton tenuissimum* (Collins) Drew, Chantransia, Rhodochorton, and Acrochaetium: 170, pl. 38, figs. 26–27, 1928. *Chantransia tenuissima* (Collins) Kylin, Calif. Rhodophyceen: 5, fig. 1 e–f, 1941.

Remarks: The combination *Acrochaetium tenuissimum* was made by Kylin (1941, p. 5) in the synonymy of *Chantransia tenuissima* and, according to Art. 40 of the International Rules, is illegitimate; and furthermore, according to Art. 45, the binomial *A. tenuissimum* (Collins) Kylin is not to be taken into consideration for purposes of priority.

Geogr. distr.: California (San Pedro) on *Zostera.*

Species Inquirendae

137. *Acrochaetium Griffithsianum* Nägeli, Morph. u. Syst. Ceram.: 406, 1861.

Geogr. distr.: England (Torquay) on *Ceramium.*

138. *Acrochaetium lanuginosum* (Dillw.) Nägeli, Morph. u. Syst. Ceram.: 405, 1861.

Geogr. distr.: England (Swansea) on *Ceramium* and other algae.

139. *Acrochaetium Pubes* (Ag.) Nägeli, Morph. u. Syst. Ceram.: 405, 1861.

Geogr. distr.: Copenhagen Sound on *Ceramium.*

140. *Acrochaetium pulvereum* Nägeli, Morph. u. Syst. Ceram.: 406, 1861.

Geogr. distr.: England (Torquay) on *Porphyra.*

141. *Acrochaetium radicans* (Harv.) J. Agardh, Anal. alg.: 48, 1892.

Geogr. distr.: Western Australia (Fremantle) on *Zostera.*

142. *Chantransia ascosperma* Reinsch, Contrib. alg. et fung.: 37, pl. 9, fig. 2, 1874–1875.

Geogr. distr.: Adriatic on various algae.

143. *Chantransia chiloensis* Reinsch, Contrib. alg. et fung.: 39, pl. 11, fig. 1, 1874–1875.

Geogr. distr.: West Indies (St. Thomas Island) on *Acanthophora.*

144. *Chantransia concava* Schmitz et Heydrich, *in* Schumann und Lauterbach, Fl. deutsch. Schutzgebiete Südsee: 24, 1901 (description *in* Heydrich, *in* Ber. deutsch. bot. Gesellsch. 10: 475, 1892, as *Chantransia secundata*).

Geogr. distr.: New Guinea on *Turbinaria.*

145. *Chantransia flagellifera* Reinsch, Contrib. alg. et fung.: 38, pl. 10, 1874–1875.

Geogr. distr.: Adriatic on *Chylocladia.*

146. *Chantransia gracillima* Reinsch, Contrib. alg. et fung.: 35, pl. 7, fig. 1, 1874–1875.

Geogr. distr.: Adriatic on *Erythroglossum.*

147. *Chantransia irregularis* Reinsch, Contrib. alg. et fung.: 32, pl. 5, fig. 1, 1874–1875.

Geogr. distr.: England (Weymouth) on *Brongniartella.*

148. *Chantransia Nordstedtiana* Reinsch, Contrib. alg. et fung.: 33, pl. 6, fig. 1, 1874–1875.

Geogr. distr.: Adriatic on *Chaetomorpha* and *Chondria.*

149. *Chantransia rigida* Reinsch, Contrib. alg. et fung.: 35, pl. 8, fig. 2, 1874–1875.

Geogr. distr.: Adriatic on *Chylocladia.*

150. *Chantransia vinculoides* Heydrich, *in* Schumann und Lauterbach, Fl. deutsch. Schutzgebiete Südsee: 25, 1901.

Geogr. distr.: New Guinea on *Sphacelaria.*

Chromastrum Papenfuss, gen. nov.

Acrochaetium, various authors (in part). *Chantransia*, various authors (in part). *Rhodochorton* various authors (in part).

Phyci microscopici, filamentis uniseriatis ramosis (raro simplicibus) effecta, pilis crebro terminantia, aut hospitis ad superficiem aut substratum alterum colligata, aut (vel in parte vel omnino) in textu hospitis sita. Cellulae filamentum uno (raro amplius) chromatophoro stellato et uno (raro aliquot) pyrenoide aut in aliquibus speciebus per speciem nullo.

Generatio asexualis cum monosporis, subinde tetrasporis.

Generatio sexualis infrequens, monoecissmo vel dioecissmo. Spermatangiis fere fasciculis parvulis super ramusculos lateralis, subinde terminales, super filamentos praecipuos. Carpogonia laterales sessiliaque super ramos erectos. Cystocarpus ex carpogonio egressens carposporangiaque singulatim ad peripheriam efficiens. Species typica: *Chromastrum virgatulum* (Harv.).

Plants microscopic, composed of branched or rarely unbranched, uniseriate filaments which frequently terminate in hairs and are attached to the surface of the host or other substratum by a single holdfast cell or a multicellular basal layer, or which are partly to almost wholly imbedded in the tissues of the host. Cells of filaments containing one or rarely more stellate chromatophores and a single or rarely a few pyrenoids, or, in certain species, apparently none.

Asexual reproduction by monospores but occasionally by tetraspores.

Sexual reproduction infrequent, monoecious or dioecious. Spermatangia usually formed in small groups on lateral branchlets, occasionally terminal on the main filaments. Carpogonia borne laterally and sessile or erect branches. Gonimoblast issuing from carpogonium and forming carposporangia singly at the periphery. Type species: *Chromastrum virgatulum* (Harv.).

Unless otherwise stated, the species in the following list reproduce asexually and by monospores only.

GROUP I. Frond epiphytic or epizoic, with a single basal cell.

1. **Chromastrum Alariae** (Jónss.) Papenfuss, comb. nov. *Chantransia Alariae* Jónsson, Mar. alg. Iceland 1: 132, fig. 1, 1901; Levring, Algenfl. norw. Westküste: 86, fig. 12, 1937. *Acrochaetium Alariae* (Jónss.) Born., Hamel, *in* Rev. Alg. 3: 177, 1928; Taylor, Mar. alg. n.-east. N. Am.: 229, 1937.

Geogr. distr.: North Atlantic on *Alaria.*

2. **Chromastrum arcuatum** (Drew) Papenfuss, comb. nov. *Rhodochorton arcuatum* Drew, Chantransia, Rhodochorton, and Acrochaetium: 165, pl. 37, figs. 1–3, 1928.

   Remarks: Reproduction sexual as well as asexual.
   Geogr. distr.: Pacific coast of North America on *Pterosiphonia* and *Sphacelaria.*

3. **Chromastrum balticum** (Rosenv.) Papenfuss, comb. nov. *Chantransia baltica* Rosenvinge, Mar. alg. Denmark 1 (1): 97, fig. 27, 1909; Levring, Algenfl. norw. Westküste: 84, fig. 11, 1937.

   Geogr. distr.: Baltic on *Polysiphonia*, west coast of Norway on *Ceramium.*

4. **Chromastrum collopodum** (Rosenv.) Papenfuss, comb. nov. *Chantransia microscopica* var. *collopoda* Rosenvinge, Deux. mém. alg. mar. Groenl.: 41, figs. 10–11, 1898. *Chantransia collopoda* (Rosenv.) Rosenvinge, Mar. alg. Denmark 1 (1): 81 (note), 1909; Levring, Algenfl. Kullen: 34, fig. 5 e–m, 1935. *Acrochaetium collopodum* (Rosenv.) Hamel, *in* Rev. Alg. 3: 175, 1928.

   Geogr. distr.: Greenland on *Chordaria* and *Laminaria*, west coast of Norway and west coast of Sweden on *Chordaria.*

5. **Chromastrum compactum** (Jao) Papenfuss, comb. nov. *Acrochaetium compactum* Jao, *in* Bull. Torrey Bot. Club 63: 241, pl. 10, figs. 6–14, 1936; Taylor, Mar. alg. n.-east. N. Am.: 228, pl. 32, figs. 6–14, 1937.

   Geogr. distr.: New England on *Cladophora.*

6. **Chromastrum crassipes** (Børgs.) Papenfuss, comb. nov. *Chantransia crassipes* Børgesen, *in* Bot. Tidsskr. 30: 1, fig. 1, 1909. *Acrochaetium crassipes* (Børgs.) Børgesen, Mar. alg. Danish W. Ind. 3 (1): 20, figs. 11–13, 1915; Taylor, Mar. alg. Florida: 134, pl. 28, fig. 16, 1928.

   Geogr. distr.: Virgin Islands, Florida, Bermuda, Canary Islands and India on a variety of algae.

7. **Chromastrum hallandicum** (Kylin) Papenfuss, comb. nov. *Chantransia hallandica* Kylin, Schwed. Chantransia-Arten: 123, fig. 8, 1906; Rosenvinge, Mar. alg. Denmark 1 (1): 93, figs. 21–23, 1909; Levring, Algenveg. Blekinge: 76, fig. 22 c–d, 1940. *Acrochaetium hallandicum* (Kylin) Hamel, *in* Rev. Alg. 3: 114, 1928 (excl. syn. *Chantransia parvula* Kylin).

   Remarks: Reproduction sexual as well as asexual.
   Geogr. distr.: North Atlantic and Baltic on a variety of algae.

8. **Chromastrum hirsutum** (Drew) Papenfuss, comb. nov. *Rhodochorton hirsutum* Drew, Chantransia, Rhodochorton, and Acrochaetium: 166, pl. 37, figs. 12–14, 1928.

   Remarks: Reproduction sexual as well as asexual.
   Geogr. distr.: Pacific coast of North America on *Polysiphonia.*

9. **Chromastrum macropus** (Kylin) Papenfuss, comb. nov. *Acrochaetium macropus* Kylin, *in* Kylin und Skottsberg, Subantark. u. antark. Meeresalg. 2: 4, fig. 2, 1919.

   Geogr. distr.: Tierra del Fuego and Falkland Islands on *Porphyra.*

10. **Chromastrum maluinum** (Hamel) Papenfuss, comb. nov. *Acrochaetium maluinum* Hamel, *in* Rev. Alg. 3: 118, 176, figs. 21–22, 1928.

    Remarks: Reproduction sexual as well as asexual.
    Geogr. distr.: Atlantic coast of France on *Porphyra.*

11. **Chromastrum microscopicum** (Näg.) Papenfuss, comb. nov. *Callithamnion microscopicum* Nägeli, *in* Kützing, Sp. alg.: 640, 1849. *Acrochaetium microscopicum* (Näg.) Nägeli, Morph. u. Syst. Ceram.: 407, figs. 24–25, 1861; Hamel, *in* Rev. Alg. 3: 109, 173, fig. 16, 1928. *Rhodochorton microscopicum* (Näg.) Drew, Chantransia, Rhodochorton, and Acrochaetium: 163, 1928.

Remarks: Reproduction sexual as well as asexual.

Geogr. distr.: Northeastern Atlantic, Mediterranean, Adriatic, and Pacific coast of North America on a variety of algae.

12. **Chromastrum moniliforme** (Rosenv.) Papenfuss, comb. nov. *Chantransia moniliformis* Rosenvinge, Mar. alg. Denmark 1 (1): 99, figs. 28–29, 1909; Levring, Algenfl. norw. Westküste: 87, 1937. *Acrochaetium moniliforme* (Rosenv.) Børgesen, Mar. alg. Danish W. Ind. 3 (1): 22, 1915. *Rhodochorton moniliforme* (Rosenv.) Drew, Chantransia, Rhodochorton, and Acrochaetium: 164, 1928.

Geogr. distr.: Denmark, Sweden, Norway, New England, northeastern Pacific, Easter Island, and Mediterranean on a variety of algae.

13. **Chromastrum parvulum** (Kylin) Papenfuss, comb. nov. *Chantransia parvula* Kylin, Schwed. Chantransia-Arten: 124, fig. 9, 1906; Levring, Algenveg. Blekinge: 75, fig. 22 a–b, 1940. *Acrochaetium parvulum* (Kylin) Hoyt, Mar. alg. Beaufort: 470, fig. 25, 1920; Børgesen, Mar. alg. Canary Isls. 3 (1): 13, fig. 6, 1927.

Geogr. distr.: North Atlantic and Baltic on a variety of algae.

14. **Chromastrum rhipidandrum** (Rosenv.) Papenfuss, comb. nov. *Chantransia rhipidandra* Rosenvinge, Mar. alg. Denmark 1 (1): 91, figs. 19–20, 1909; Kylin, *in* Lunds Univ. Årsskr. N. F. Avd. 2, 24 (4): 5, figs. 1–2, 1928; Levring, Algenfl. norw. Westküste: 83, 1937. *Acrochaetium rhipidandrum* (Rosenv.) Hamel, *in* Rev. Alg. 3: 119, 176, fig. 23, 1928.

Remarks: Reproduction sexual as well as asexual.

Geogr. distr.: Denmark, west coast of Norway and Atlantic coast of France on *Porphyra.*

15. **Chromastrum unifilum** (Jao) Papenfuss, comb. nov. *Acrochaetium unifilum* Jao, *in* Bull. Torrey Bot. Club 63: 239, pl. 10, figs. 26–32, 1936; Taylor, Mar. alg. n.-east. N. Am.: 228, pl. 32, figs. 26–32, 1937.

Geogr. distr.: New England on *Arthrocladia.*

GROUP II. Frond epiphytic or epizoic, with a multicellular basal layer.

16. **Chromastrum Boergesenii** (Schiffn.) Papenfuss, comb. nov. *Acrochaetium Børgesenii* Schiffner, *in* Hedwigia 71: 143, fig. 1, 1931.

Remarks: Reproductive organs unknown.

Geogr. distr.: Adriatic on *Chaetomorpha.*

17. **Chromastrum Duboscqii** (Feldm.) Papenfuss, comb. nov. *Acrochaetium Duboscqii* Feldmann, *in* Bul. Soc. Hist. Nat. Afr. Nord 26: 366, 1935.

Geogr. distr.: Mediterranean on *Bryopsis* and *Chaetomorpha.*

18. **Chromastrum floridulum** (Dillw.) Papenfuss, comb. nov. *Conferva floridula* Dillwyn, Br. conf.: 73, pl. F, 1802. *Rhodochorton floridulum* (Dillw.) Nägeli, Morph. u. Syst. Ceram.: 358, fig. 2, 1861; Kuckuck, Beitr. Kenntn. Meeresalg.: 21, fig. 6, 1897; Hamel, *in* Rev. Alg. 3: 146, 199, figs. 37, 39 f, 1928.

Remarks: Asexual reproduction by tetraspores.
Geogr. distr.: Atlantic coast of Europe on sand-covered rocks.

19. **Chromastrum humile** (Rosenv.) Papenfuss, comb. nov. *Chantransia humilis* Rosenvinge, Mar. alg. Denmark 1 (1): 117, figs. 44–45, 1909; Levring, Algenfl-norw. Westküste: 89, 1937; Algenveg. Blekinge: 78, fig. 23 a–b, 1940. *Acrochaetium humile* (Rosenv.) Børgesen, Mar. alg. Danish W. Ind. 3 (1): 23, 1915.

Geogr. distr.: Denmark, Baltic, west coasts of Sweden and Norway on a variety of

20. **Chromastrum Macula** (Rosenv.) Papenfuss, comb. nov. *Chantransia Macula* Rosenvinge, Mar. alg. Denmark 1 (1): 114, fig. 42, 1909. *Acrochaetium Macula* (Rosenv.) Hamel, *in* Rev. Alg. 3: 191, 1928.

Geogr. distr.: Denmark and west coast of Norway on *Polysiphonia.*

21. **Chromastrum polyblastum** (Rosenv.) Papenfuss, comb. nov. *Chantransia polyblasta* Rosenvinge, Mar. alg. Denmark 1 (1): 115, fig. 43, 1909; Levring, Algenfl. Kullen: 37, 1935. *Acrochaetium polyblastum* (Rosenv.) Børgesen, Mar. alg. Danish W. Ind. 3 (1): 23, 1915.

Remarks: Asexual reproduction by tetraspores.
Geogr. distr.: Denmark and west coast of Sweden on a variety of algae.

22. **Chromastrum pulchellum** (Børgs.) Papenfuss, comb. nov. *Acrochaetium pulchellum* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 23, figs. 14–16, 1915.

Geogr. distr.: Virgin Islands on *Chaetomorpha.*

23. **Chromastrum secundatum** (Lyngb.) Papenfuss, comb. nov. *Callithamnion Dawiesii β secundatum* Lyngbye, Tent. hydrophyt. Dan.: 129, pl. 41, fig. B 4–6, 1819. *Acrochaetium secundatum* (Lyngb.) Nägeli, Morph. u. Syst. Ceram.: 405, 1861; Newton, Br. seaweeds: 254, 1931; Taylor, Mar. alg. n.-east. N. Am.: 230, pl. 31, figs. 1–3, 1937. *Chantransia secundata* (Lyngb.) Thur., Børgesen, Mar. alg. Faröes: 350, fig. 51, 1902; Kylin, Algenfl. schwed. Westküste: 115, fig. 24, 1907.

Remarks: Asexual reproduction by tetraspores as well as monospores.
Geogr. distr.: North Atlantic on a variety of algae, Adriatic on *Peyssonelia.*

24. **Chromastrum sessile** (Nakam.) Papenfuss, comb. nov. *Rhodochorton sessile* Nakamura, Rhodochorton fr. Japan 1: 278, fig. 4, 1941.

Geogr. distr.: Japan on *Hyalosiphonia.*

25. **Chromastrum virgatulum** (Harv.) Papenfuss, comb. nov. *Callithamnion virgatulum* Harvey, *in* Hooker, Eng. fl. 5: 349, 1833. *Acrochaetium virgatulum* (Harv.) J. Ag., Børgesen, Mar. alg. Canary Isls. 3 (1): 14, figs. 7–8, 1927; Hamel, *in* Rev. Alg. 3: 139, 190, fig. 35, 1928 (excl. f. *secundata*); Taylor, Mar. alg. n.-east. N. Am.: 230, 1937. *Chantransia virgatula* (Harv.) Thur., Børgesen, Mar. alg. Faeröes: 351, figs. 52–54, 1902; Rosenvinge, Mar. alg. Denmark 1 (1): 109, figs. 37–38, 1909 (excl. f. *secundata*).

Remarks: Asexual reproduction by tetraspores as well as monospores.
Geogr. distr.: North Atlantic, Baltic, and Mediterranean on various algae and marine angiosperms.

GROUP III. Frond partially to almost wholly endophytic or endozoic.

26. **Chromastrum cytophagum** (Rosenv.) Papenfuss, comb. nov. *Chantransia cytophaga* Rosenvinge, Mar. alg. Denmark 1 (1): 121, figs. 50–51, 1909; Levring, Algenfl. Kullen: 39, 1935. *Acrochaetium cytophagum* (Rosenv.) Hamel, *in* Rev. Alg. 3: 185, 1928.

 Geogr. distr.: Denmark and west coast of Sweden in *Porphyra.*

27. **Chromastrum Dumontiae** (Rosenv.) Papenfuss, comb. nov. *Chantransia Dumontiae* Rosenvinge, Mar. alg. Denmark 1 (1): 124, fig. 52, 1909. *Acrochaetium Dumontiae* (Rosenv.) Hamel, *in* Rev. Alg. 3: 185, 1928.

 Remarks: Asexual reproduction by tetraspores.
 Geogr. distr.: Denmark in *Dumontia.*

28. **Chromastrum immersum** (Rosenv.) Papenfuss, comb. nov. *Chantransia immersa* Rosenvinge, Mar. alg. Denmark 1 (1): 130, figs. 56–58, 1909; Levring, *in* Bot. Notiser 1935: 459, fig. 2, 1935. *Acrochaetium immersum* (Rosenv.) Hamel, *in* Rev. Alg. 3: 186, 1928.

 Geogr. distr.: Denmark in *Rhodomela* and *Polysiphonia*, west coast of Sweden in *Polysiphonia.*

29. **Chromastrum implicatum** (Drew) Papenfuss, comb. nov. *Rhodochorton implicatum* Drew, Chantransia, Rhodochorton, and Acrochaetium: 190, pl. 46, figs. 76–78, 1928.

 Geogr. distr.: California in *Halosaccion.*

30. **Chromastrum infestans** (Howe et Hoyt) Papenfuss, comb. nov. *Acrochaetium infestans* Howe et Hoyt, *in* Mem. New York Bot. Gard. 6: 116, pl. 14, 1916; Hoyt, Mar. alg. Beaufort: 473, pl. 118, 1920.

 Geogr. distr.: North Carolina in various hydroids, North Africa in the bryozoan *Zoobotryon.*

31. **Chromastrum Liagorae** (Børgs.) Papenfuss, comb. nov. *Acrochaetium Liagorae* Børgesen, Mar. alg. Danish W. Ind. 3 (1): 58, figs. 60–62, 1915. *Chantransia Liagorae* Børgesen, *ibid.*: 57 [not *Chantransia Liagorae* Web.-v. Bosse, 1914, p. 275, nor *Acrochaetium Liagorae* (Web.-v. Bosse) Hamel, 1928, p. 185]. *Acrochaetium Collinsianum* Børgesen, Mar. alg. Danish W. Ind. 3 (6): 454, 1920; Taylor, Mar. alg. Florida: 134, pl. 20, fig. 6, 1928.

 Remarks: Børgesen (1920*a*, p. 454) believed that the binomial *Chantransia Liagorae* Weber-van Bosse (1914) invalidated his (Børgesen, 1915) *Acrochaetium Liagorae* and consequently renamed his species *A. Collinsianum;* and this name has been accepted by subsequent writers. The binomial *A. Liagorae* Børgs. is, however, perfectly valid. In 1928 Hamel transferred *Chantransia Liagorae* Web.-v. Bosse to *Acrochaetium*, but he apparently had overlooked the earlier homonym of *A. Liagorae* Børgs. Since the species of Weber-van Bosse seems to belong to *Acrochaetium* in the sense of the present article, it is necessary to replace the specific epithet. The name *Vanbosseae* is proposed as a substitute. It may be noted that Børgesen (1915), on page 57 of the third part of his Marine Algae of the Danish West Indies, by oversight had called his plant *Chantransia Liagorae.* This binomial is a homonym of *C. Liagorae* Web.-v. Bosse (1914). On the next page of this work, however, Børgesen used the name *Acrochaetium Liagorae* in connection with the explanation of the figures. This validates the latter binomial.
 Geogr. distr.: Virgin Islands and Florida in *Liagora.*

32. **Chromastrum Liagoroides** (Børgs.) Papenfuss, comb. nov. *Acrochaetium Liagoroides* Børgesen, *in* Jour. Indian Bot. Soc. 16: 40, figs. 24–25, 1937.

    Remarks: Asexual reproduction by tetraspores.
    Geogr. distr.: Southern India in *Liagora.*

33. **Chromastrum Porphyrae** (Drew) Papenfuss, comb. nov. *Rhodochorton Porphyrae* Drew, Chantransia, Rhodochorton, and Acrochaetium: 188, pl. 46, figs. 70–75, 1928. *Acrochaetium Porphyrae* (Drew) Smith, Mar. alg. Monterey Penin.: 179, pl. 40, figs. 8–9, 1944.

    Geogr. distr.: California in *Porphyra.*

34. **Chromastrum Stilophorae** (Levring) Papenfuss, comb. nov. *Chantransia Stilophorae* Levring, Algenfl. Kullen: 39, fig. 8 a–e, 1935.

    Geogr. distr.: West coast of Sweden in *Stilophora.*

Audouinella Bory

Bory, *in* Dict. class. hist. nat. 3: 340, 1823 (as *Auduinella*). *Chantransia,* various authors (in part, not of De Candolle). *Acrochaetium,* various authors (in part). *Rhodochorton,* various authors (in part).

Thalli microscopic, composed of branched, uniseriate filaments which may end in hairs and which issue from a creeping, unistratose or pulvinate basal portion. Cells of filaments containing one to a few spiral chromatophores without pyrenoids.

Asexual reproduction by mono- or tetraspores.

Sexual reproduction infrequent, monoecious or dioecious; the sexual generation alternating, as far as known, with an asexual generation. Spermatangia occurring in clusters on lateral branchlets. Carpogonia borne laterally and sessile on erect branches, terminally on one- or two-celled branchlets, or intercalary in origin. Gonimoblast developing directly from the carpogonium and forming solitary or seriate carposporangia at the terminal ends of its branches.

Type species: *Audouinella Hermanni* (Roth) Duby.

Unless otherwise stated, the species in the following list reproduce asexually and by monospores only.

Fresh-water Species

1. **Audouinella eugenea** (Skuja) Papenfuss, comb. nov. *Chantransia eugenea* Skuja, *in* Beihefte bot. Centralbl. 52 (2): 177, pl. 1, figs. 3–5, 1934.

    Geogr. distr.: India (Punjab) on aquatics.

2. *Audouinella Hermanni* (Roth) Duby, De Toni, Syll. alg. 4 (4): 1865, 1905; Hamel, *in* Rev. Alg. 2 (1): 46, fig. 8 a, 1925.

    Geogr. distr.: Europe and North America on algae and other aquatic plants.

3. **Audouinella mstinensis** (Kom.) Papenfuss, comb. nov. *Chantransia mstinensis* Komarov, Jour. Soc. Bot. Russie 1: 100, fig. 4, 1916.

    Geogr. distr.: Russia (Msta River at Novgorod) on *Lemanea.*

4. **Audouinella subtilis** (Möb.) Papenfuss, comb. nov. *Chantransia subtilis* Möbius, Austr. Süsswasseralg. 2: 313, pl. 1, figs. 9–10, 1894.

    Geogr. distr.: Australia on *Nitella.*

5. **Audouinella tenella** (Skuja) Papenfuss, comb. nov. *Chantransia tenella* Skuja, *in* Beihefte bot. Centralbl. 52 (2): 177, pl. 1, figs. 1–2, 1934.

Remarks: This species is based upon material which was collected in California by the late Professor Gardner. Skuja (*loc. cit.*) gave as the locality "Mt. Tamalpais, Mariubo." This should read "Mt. Tamalpais, Marin Co[unty]." According to the notes in Gardner's field book, the material was secured "on rocks wet with dripping water, by railroad track about halfway up Mt. Tamalpais."

Geogr. distr.: California (Mount Tamalpais) on rocks.

6. *Audouinella violacea* (Kütz.) Hamel, *in* Rev. Alg. 2 (1): 46, 1925. *Chantransia violacea* Kütz., De Toni, Syll. alg. 4 (4): 1866, 1905. *Rhodochorton violaceum* (Kütz.) Drew, *in* Ann. Bot. 49: 439, figs. 1–19, 1935. *Chantransia Boweri* Murray et Barton, *in* Jour. Linn. Soc. Bot. 28: 213, pls. 36–37, 1891. *Audouinella Boweri* (Murr. et Bart.) Hamel, *in* Rev. Alg. 2 (1): 47, 1925.

Remarks: Drew in 1936 showed that the *Chantransia Boweri* of Murray and Barton is co-specific with *Audouinella violacea*. Reproduction is sexual as well as asexual by both monospores and tetraspores.

Geogr. distr.: Northern hemisphere on *Lemanea* and on stones.

Marine Species

7. **Audouinella efflorescens** (J. Ag.) Papenfuss, comb. nov. *Callithamnion efflorescens* J. Agardh, Sp. alg. 2 (1): 15, 1851. *Acrochaetium efflorescens* (J. Ag.) Nägeli, Morph. u. Syst. Ceram.: 405, 1861; Hamel, *in* Rev. Alg. 3: 196, 1928. *Chantransia efflorescens* (J. Ag.) Kjellm., Lehmann, Chantransia efflorescens: 1–8, pl. 1, 1902; Kylin, Schwed. Chantransia-Arten: 113, figs. 1–5, 1906; Rosenvinge, Mar. alg. Denmark 1 (1): 134, figs. 61–64, 1909; Levring, Algenveg. Blekinge: 80, 1940. *Rhodochorton efflorescens* (J. Ag.) Drew, Chantransia, Rhodochorton, and Acrochaetium: 151, 1928.

Remarks: Reproduction sexual as well as asexual by monospores and tetraspores.

Geogr. distr.: Arctic, eastern North Atlantic, and Baltic on a variety of algae, on animals, and on rocks.

8. **Audouinella membranacea** (Magnus) Papenfuss, comb. nov. *Callithamnion* (*Rhodochorton*) *membranaceum* Magnus, Bot. Ergeb. Nordseefahrt 1872: 67, pl. 2, figs. 7–15, 1874. *Rhodochorton membranaceum* (Magnus) Hauck, Meeresalg.: 69, 1885 (only as to binomial); Kuckuck, Beitr. Kenntn. Meeresalg.: 13–24, figs. 1–4, 7, 1897; Rosenvinge, Mar. alg. Denmark 3: 393, figs. 331–335, 1923–1924; Drew, Chantransia, Rhodochorton, and Acrochaetium: 186, 1928; Hamel, *in* Rev. Alg. 3: 152, 202, fig. 39 a–e, 1928; Taylor, Mar. alg. n.-east. N. Am.: 240, pl. 31, figs. 11–12, 1937.

Remarks: Reproduction asexual by tetraspores.

Geogr. distr.: Baltic, North Atlantic, and Pacific coast of North America on various hydroids.

9. **Audouinella pectinata** (Kylin) Papenfuss, comb. nov. *Chantransia pectinata* Kylin, Schwed. Chantransia-Arten: 120, figs. 6–7, 1906; Rosenvinge, Mar. alg. Denmark 1 (1): 138, figs. 65–66, 1909. *Acrochaetium pectinatum* (Kylin) Hamel, *in* Rev. Alg. 3: 197, 1928.

Remarks: Reproduction asexual by monospores and tetraspores.

Geogr. distr.: West coast of Sweden and Denmark on a variety of algae and on animals.

Rhodochorton Näg.

Nägeli, Morph. u. Syst. Ceram.: 355, 1861. *Thamnidium* Thuret, *in* Le Jolis, Alg. mar. Cherbourg: 110, 1863.

Thalli microscopic to one cm. or more in length, composed of a disklike or creeping basal portion from which issue erect, branched, uniseriate filaments, whose cells contain a few to many discoid chromatophores without pyrenoids.

Asexual reproduction by tetraspores formed in cruciately divided sporangia, which are terminal or lateral in position.

Sexual reproduction unknown except in *R. penicilliforme*, whose spermatangia have been recorded.

Type species: *Rhodochorton purpureum* (Lightf.) Rosenv.

1. *Rhodochorton concrescens* Drew, Chantransia, Rhodochorton, and Acrochaetium: 167, pl. 37, fig. 15, 1928; Smith, Mar. alg. Monterey Penin.: 183, pl. 41, figs. 3–4, 1944.

   Geogr. distr.: California on the hydroids *Abietinaria* and *Sertularella*.

2. *Rhodochorton corynosporoides* Hamel, *in* Rev. Alg. 3: 198, 202, fig. 44 g, 1928. *Callithamnion corynosporoides* Crouan, *in* Mazé et Schramm, Alg. Guadeloupe: 144, 1870–1877 (*nomen nudum*).

   Geogr. distr.: Guadeloupe on *Centroceras*.

3. *Rhodochorton islandicum* Rosenvinge, *in* Bot. Tidsskr. 23: 75, figs. 1–4, 1900.

   Remarks: Børgesen (1902, p. 391) has studied a form of *Rhodochorton purpureum* (= *R. Rothii*) from the Faroe Islands which resembles *R. islandicum*, and he is somewhat doubtful if the latter species is actually distinct from *R. purpureum*.

   Geogr. distr.: Iceland on rocks above tide level.

4. *Rhodochorton penicilliforme* (Kjellm.) Rosenvinge, Alg. mar. Groenl.: 66, fig. 9, 1894; Deux. mém. alg. mar. Groenl.: 23, 1898; Mar. alg. Denmark 3: 388, figs. 325–327, 1923–1924; Kylin, Mar. red alg. Friday Harbor: 45, fig. 26 a–c, 1925; Drew, Chantransia, Rhodochorton, and Acrochaetium: 176, 1928; Miranda, Alg. mar. côtes la Manche: 279, fig. 3, 1932; Taylor, mar. alg. n.-east. N. Am.: 239, 1937.

   Geogr. distr.: North Atlantic and Pacific coast of North America on algae and hydroids.

5. *Rhodochorton purpureum* (Lightf.) Rosenvinge, *in* Bot. Tidsskr. 23: 75, 1900; Hamel, *in* Rev. Alg. 3: 151, 201, 1928. *Byssus purpurea* Lightfoot, Fl. Scotica 2: 1000, 1777. *Rhodochorton Rothii* (Turt.) Nägeli, Morph. u. Syst. Ceram.: 356, pl. 1, figs. 1, 3, 1861 (not as to type); Børgesen, Mar. alg. Faeröes: 390, figs. 61–65, 1902; Rosenvinge, Mar. alg. Denmark 3: 390, figs. 328–330, 1923–1924 (excl. syn. *Conferva Rothii* Turton); Hamel, *in* Rev. Alg. 3: 147, 199, fig. 38, 1928 (excl. syn. *Conferva Rothii* Turton); Drew, Chantransia, Rhodochorton, and Acrochaetium: 177, 1928 (excl. syn. *Conferva Rothii* Turton); Taylor, Mar. alg. n.-east. N. Am.: 239, pl. 45, figs. 1–2, 1937. *Rhodochorton intermedium* (Kjellm.) Kjellman, Alg. Arctic Sea: 184, pl. 15, fig. 8, 1883; Hamel, *in* Rev. Alg. 3: 200, 1928. *Thamnidium intermedium* Kjellman, Spetsb. thalloph. 1: 28, fig. 10, 1875. *Rhodochorton parasiticum* Batters, *in* Jour. Bot. 34: 389, 1896. *Conferva violacea* Roth, Cat. bot. Fasc. 1: 190, pl. 4, fig. 1, 1797

(not *Conferva violacea* Hudson, 1778, p. 592, nor *Ceramium violaceum* Roth, 1797, p. 150, nor *Conferva Rothii* Turton, 1806, p. 1809).

Remarks: In agreement with Harvey (1846) and other early writers, *Rhodochorton purpureum* and the plant commonly known as *R. Rothii* are here considered as synonymous. If, however, these two entities actually are distinct species, as Rosenvinge (1900) and others believe, the binomial *R. Rothii* will have to be replaced with another, since it is based on *Conferva Rothii* Turton, which applies to a species of *Polysiphonia*—not of *Rhodochorton*, as has been supposed.

This curious error in the nomenclature of *Rhodochorton Rothii* dates back to Dillwyn (1802–1809, p. 73 and the text to pl. 73) and has persisted to this day. Turton (1806, p. 1809) proposed the name *Conferva Rothii* as a substitute for *Ceramium violaceum* Roth 1797, p. 150), which is a species of *Polysiphonia*, and not for *Conferva violaceum* Roth (1797, p. 190), which is a species of *Rhodochorton* in the sense of Nägeli, as Dillwyn believed.

The perpetuation of this error may be owing to the fact that Turton's "General System of Nature" is generally unavailable and in consequence has usually been cited from Dillwyn. The following extracts from Turton and Roth will show that *Conferva Rothii* Turton is based upon *Ceramium violaceum* Roth. The passage from Turton (p. 1809) reads: "[*Conferva*] *Rothii*. Branchlets forked, fascicled: joints oblong, striate, with pellucid rather elevated partitions: capsules globular, lateral. Roth Cat bot. 1. t. 8. 2." and the diagnosis in Roth (p. 150) reads: "3. *Ceramium violaceum* filamentis cartilagineis, dichotomis, ramosissimis, geniculatis: ramulis fasciculatis: geniculis annularibus, subeleuatis, pellucidis; articulis oblongis striatis, capsulis globosis, lateralibus, sessilibus. Tab. VIII. fig. 2."

In considering *Conferva Rothii* as the equivalent of *Conferva violacea* Roth rather than of *Ceramium violaceum* Roth, Dillwyn not only misapplied the binomial of Turton, but was under the delusion that Turton had proposed the new name on account of the existence of the earlier homonym of *Conferva violacea* Hudson (1778, p. 592). It is clear, however, that Turton was not aware of this binomial of Hudson, for on page 1812 of his "System of Nature" he listed as a species of *Conferva* the *C. violacea* of Roth. Upon transferring *Ceramium violaceum* to *Conferva*, it thus was necessary for Turton to propose a new specific name.

Hamel (1928*b*, p. 200) accepts *Rhodochorton intermedium* as an autonomous species, but in agreement with Jónsson (1901, p. 146) and Børgesen (1902, p. 394) it seems best to consider this species as synonymous with *R. purpureum* (or *R. Rothii* of these writers). Rosenvinge (1926, p. 34) has also remarked that *R. intermedium* can ". . . scarcely be kept distinct from *Rh. Rothii*."

Geogr. distr.: Widely distributed in the northern hemisphere, usually on rocks but also on algae, bryozoans, and wood.

6. *Rhodochorton spetsbergense* (Kjellm.) Kjellman, Alg. Arctic Sea: 187, 1883. *Thamnidium spetsbergense* Kjellman, Spetsb. thalloph. 1: 31, figs. 11–12, 1875.

Geogr. distr.: Arctic Sea on *Chaetomorpha*.

7. *Rhodochorton subsimplex* (Harv. ex J. Ag.) De Toni, Syll. alg. 4 (3): 1515, 1903; Kylin, Mar. red alg. Friday Harbor: 45, fig. 25 f–g, 1925.

Geogr. distr.: Tonga Islands on wood.

8. *Rhodochorton tenue* Kylin, Mar. red alg. Friday Harbor: 44, fig. 25 b–e, 1925; Drew, Chantransia, Rhodochorton, and Acrochaetium: 177, pl. 40, fig. 33, 1928.

Geogr. distr.: Pacific coast of North America on rocks.

Species Inquirendae

9. *Rhodochorton Galaxaurae* Vickers, Alg. mar. Barbade: 64, 1905.

Geogr. distr.: Barbados.

10. *Rhodochorton Hauckii* Hamel, *in* Rev. Alg. 3: 155, 203, 1928. *Acrochaetium Hauckii* Schiffner, Alg. adriat. Meeres: 133, 1916 (in part).

Geogr. distr.: Adriatic on algae.

11. *Rhodochorton Welwitschii* (J. Ag.) De Toni, Syll. alg. 4 (3): 1515, 1903.

Geogr. distr.: Portugal.

Species Excludendae

Rhodochorton constrictum (Hering) De Toni, Syll. alg. 4 (3): 1514, 1903 = *Pleonosporium constrictum* (Hering) Nägeli, Morph. u. Syst. Ceram.: 342, 1861.

Remarks: The writer has examined the Hering material of this species which is in Herb. Berlin and found it to be a species of *Pleonosporium*.

Geogr. distr.: South Africa.

Rhodochorton speluncarum Collins et Hervey, Alg. Bermuda: 147, 1917 = *Spermothamnion speluncarum* (Collins et Hervey) Howe, *in* Britton and Millspaugh, Bahama fl.: 578, 1920.

Geogr. distr.: Burmuda and the Bahama Islands.

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III. A TAXONOMIC ORGANIZATION OF THE GENUS

BY

T. H. GOODSPEED

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THE IDENTITY of the Linnean genus *Nicotiana* remains essentially intact even though most of the species which now compose it have since been described. The first considerable accession to the original group of seven species was proposed in 1818 by Lehmann, who dealt with twenty-one. In the same year, Kunth made an attempt to organize the genus. On the basis of form of corolla and character of limb he arranged the seven species he dealt with under two subdivisions. Somewhat later, Don (1838), who discussed thirty-three species, proposed the taxonomic framework of *Nicotiana* which, with modifications, is still current. He recognized four sections based upon shape and color of corolla: I, *Tabacum;* II, *Rustica;* III, *Petunioides;* IV, *Polydiclia.* From the modern viewpoint, Don's first section included only varieties of *N. tabacum* L., and his second consisted of varieties of *N. rustica* L. together with *N. paniculata* L., *N. undulata* R. and P., *N. glauca* Grah., and *N. langsdorffii* Weinm. apud Roem. and Schult. In his section III, twelve species were accumulated which are referable to the following modern species: *N. alata* Link and Otto, *N. bonariensis* Lehm., *N. longiflora* Cav., *N. noctiflora* Hook., *N. acuminata* (Grah.) Hook., *N. suaveolens* Lehm., and *N. repanda* Willd. Section IV contained *N. nana* Lindl., *N. quadrivalvis* Pursh., and *N. multivalvis* Lindl. The first of these is today referred to the genus *Nierembergia,* and the two others are considered to be varieties of *N. bigelovii* (Torr.) Wats. In addition, Don erected the genus *Sairanthus* for *N. glutinosa* L. and assigned *N. tomentosa* R. and P. to *Lehmannia* of Sprengel. Dunal (1852) placed the genera *Nicotiana, Lehmannia, Petunia, Leptophragma,* and *Vestia* in his subtribe Nicotianeae. His organization of *Nicotiana* is a reflection of that of Don since he recognized section *Polydiclia* and his remaining section, *Didiclia,* contained only *Tabacum, Rustica,* and *Petunioides* as subdivisions. By contrast with Wettstein (1895), who retained only the first three of Don's sections and reduced *Lehmannia* to synonomy, Comes (1899) recognized all four of the Donian sections and retained *Lehmannia.* In 1929 Capus, Lenelliot, and Foëx returned to the four divisions of Don and referred to all the species they knew as varieties of *N. rustica, N. petunioides, N. polydiclia,* or *N. tabacum.*

The work of Splendore (1906) and of Anastasia (1914) introduced the modern view on problems of phylesis in *Nicotiana.* Derived from their rather intensive but largely morphological investigations were hypotheses concerning the evolution of the genus, based in part on the postulate that certain species were of hybrid derivation. During the period 1912–1930, studies of many species of *Nicotiana* by a number of investigators provided cytological and genetic evidence which has implemented a mode of attack upon phylogenetic problems in *Nicotiana* foreshadowed by Splendore's and Anastasia's hypotheses. In this laboratory the taxonomic organization of the genus by Setchell (1912), which corresponded to that of Wettstein, supplied a background for cytogenetic analyses of the large living collection of species of *Nicotiana* which he had assembled (cf. Goodspeed, 1945). In 1928 East referred to the presence in the genus of a "number of genetic centers," a suggestion which anticipated the formulation by the author of a "genetic group" concept in terms of which he discussed evidence of phylesis in *Nicotiana* (1934). Ultimately (1942) he recognized the following "genetic groups": the ACUMINATA, the ALATA, the CAVANILLESII, the PANICULATA, the REPANDA, the SUAVEOLENS, and the TOMENTOSA. Recently, Kostoff (1943) divided the genus into eight "sections," to seven of which he gave the same designations as those the author had previously applied to his "genetic groups." The taxonomic treatment of *Nicotiana* in what follows contains eleven sections, under three subgenera, most of which carry the same designations as the "genetic groups" and the "sections" of Kostoff. The latter are not, however, recognized since they lack descriptions. It is also to be noted that the species which constitute seven of Kostoff's sections are not the same as those of the same name in the following taxonomic organization. For example, the "section Tomentosa" of Kostoff consists of *N. tomentosa*, *N. tomentosiformis*, *N. glutinosa*, *N. wigandioides*, *N. tabacum*, and *N. sylvestris*, whereas the author's section *Tomentosae* is made up of the first three of those species together with *N. setchellii* and *N. otophora.*

Except for the inflorescence, the diagnosis by Bentham and Hooker (1876) of the genus is adequate. Descriptions of the classical species are given by Dunal (1852), Comes (1899), Setchell (1912), and Grabovetzkaya (1937). Their distribution is commented upon by Goodspeed (1941, 1942) and Grabovetzkaya (*l.c.*). Taxonomy and distribution of the Australian–South Pacific species are treated by Wheeler (1935).

TAXONOMIC ORGANIZATION

Subgenus ***Rustica*** (Don) Goodspeed, stat. nov.

Section *Rustica* Don, Gen. Syst. 4, p. 464 (1838)
Type: *Nicotiana rustica* L.

Stout herbs or short-lived shrubs; leaves usually petioled; panicle columnar or spreading. corolla regular, tubular or tubular-salverform, limb green or yellowish, obsolescently lobed.

Section PANICULATAE Goodspeed, sect. nov.

Herbae firmae aut frutices paulum lignosi; foliis petiolatis, ovatis v. cordatis; panicula columnari v. patula; corolla certe duplo longiore quam latiore, tubulosa v. tubuloso-hypocrateriformi, limbo viridi flavescenteve, staminibus aequalibus v. subaequalibus, ad corollam infime aequaliter affixis. Typus: *Nicotiana paniculata* L.

Stout herbs or soft-woody shrubs; leaves petioled, ovate to cordate; panicle columnar or spreading; corolla at least twice as long as broad, tubular or tubular-salverform, limb green or yellowish; stamens equal or nearly so, equally inserted low on corolla. Type: *N. paniculata* L. Other members: *N. knightiana* Goodsp., *N. solanifolia* Walp., *N. benavidesii* Goodsp., *N. raimondii* Macbr., *N. cordifolia* Phil., *N. glauca* Grah.

All six species clearly interrelated: *N. paniculata* and *N. knightiana* show close morphological affinity in majority of characters, while resemblance in flower relates *N. raimondii* to *N. cordifolia* and *N. solanifolia* to *N. benavidesii.* In leaf shape and habit (exclusive of inflorescence) *N. benavidesii* approaches *N. glutinosa* of subgenus *Tabacum,* section *Tomentosae.* Structure of inflorescence, increased longevity, and woodiness sets *N. glauca* somewhat apart. Of *N. glauca* (var. *lateritia*) and *N. cordi-*

folia maroon- or purple-flowered races are known. Four species are Peruvian: *N. benavidesii* and *N. raimondii* peculiar to southern Andes, *N. paniculata* Andean and coastal, *N. knightiana* restricted to south coastal lomas. *N. solanifolia* is of limited distribution in fog belt of northern coastal Chile, *N. glauca* native to northwestern Argentina, and *N. cordifolia* endemic on Mas a Fuera of Juan Fernandez group. Habitat, commonly arid to semiarid. Chromosome number, 12 pairs.

Section THYRSIFLORAE Goodspeed, sect. nov.

Herbae perennes magnae; foliis sessilibus v. subsessilibus, oblanceolatis; panicula columnari; corolla late obconico-tubulosa, longitudine et latitudine fere aequali, limbo viridulo-flavescente; staminibus aequalibus, inclusis, infra medium corollae aequaliter affixis. Typus: *Nicotiana thyrsiflora* Goodsp.

Large perennial herbs; leaves sessile or nearly so, oblanceolate; panicle columnar; corolla broadly obconic-tubular, the length and breadth approximately equal, limb greenish yellow; stamens equal, included, equally inserted below middle of corolla. Type: *N. thyrsiflora* Goodsp.

The single species, *N. thyrsiflora*, is distinguished from other sections of the subgenus by its spicate habit. Long, narrow, crowded, glabrous leaves form rosulate base and densely clothe almost simple, erect stems which pass into long, columnar panicles. In flower it resembles *N. rustica*; upright limb and purple anthers superficially suggest *N. langsdorffii*, an anomalous member of section *Alatae*, subgenus *Petunioides*. It is endemic in highlands of northwestern Peru. Habitat, somewhat arid but less so than that of preceding section. Chromosome number, 12 pairs.

Section RUSTICAE Goodspeed, sect. nov.

Herbae, saepe firmae; foliis petiolatis, ovatis, ovato-oblongis v. cordatis; panicula patula aut paulum columnari; corolla tubulato-hypocrateriformi, longitudine et latitudine fere aequali, limbo viridulo-flavescente; staminibus omnibus inclusis, uno quam alteris breviore, infra medium corollae affixis. Typus: *Nicotiana rustica* L.

Herbs, commonly stout; leaves petioled, ovate, ovate-oblong, or cordate; panicle spreading or somewhat columnar; corolla tubular-salverform, the length and width nearly equal, limb greenish yellow; stamens all included, one shorter, inserted below middle of corolla. Type: *N. rustica* L.

Like the section *Thyrsiflorae*, this one contains a single species; unlike it, it exhibits a wide range of polymorphism, extremes of which relate *N. rustica* to *N. paniculata*, section *Paniculatae*, and to *N. undulata*, section *Undulatae*. Cytogenetic evidence points to those two species or progenitors as having entered into the amphidiploid origin of *N. rustica*, all three species having today a common center of distribution in central Andean Peru. The species is often but not exclusively associated with evidence of civilization. It has been introduced in North America, Africa, and elsewhere. Chromosome number, 24 pairs.

Subgenus *Tabacum* (Don) Goodspeed, stat. nov.

Section *Tabacum* Don, Gen. Syst. 4, p. 462 (1838)

Type: *Nicotiana tabacum* L.

Stout herbs or short-lived subarborescent shrubs; leaves large and commonly decurrent, rarely petiolate; panicles broadish compact or spreading; corolla regular or zygomorphic with throat gaping, inflated above into cup, cylinder, or inverted cone, the limb commonly white to red, slightly to somewhat lobed.

Section TOMENTOSAE Goodspeed, sect. nov.

Frutices vitae breves subarborescentes, raro herbae; foliis, vulgo decurrentibus ovato-lanceolatis, alato-petiolatis, raro cordato-petiolatis; inflorescentia vulgo paniculata semel-composita lata; corolla zygomorpha, clare curvata, campanulato-hypocrateriformi, longitudine et latitudine fere aequali, limbo albo v. rubro (aliquando flavovirenti), leviter v. profunde lobato, staminibus inaequalibus, vulgo conspicue exsertis, ad v. prope basim corollae aequaliter affixis. Typus: *Nicotiana tomentosa* R. & P.

Short-lived subarborescent shrubs, rarely herbs; leaves commonly ovate-lanceolate, decurrent, winged-petiolate, rarely cordate, petiolate; inflorescence usually a once-compound broadish panicle; corolla zygomorphic, distinctly curved, campanulate-salverform, in length and width approximately equal, limb white to red (sometimes yellowish green), slightly to strongly lobed; stamens unequal, generally prominently exserted, equally inserted at or near base of corolla. Type: *N. tomentosa* R. & P. Other members: *N. tomentosiformis* Goodsp., *N. otophora* Griseb., *N. setchellii* Goodsp., *N. glutinosa* L.

N. tomentosa, *N. tomentosiformis*, and *N. otophora* are closely related in habit, leaf, inflorescence, and flower. They are few- to several-stemmed perennials, subarborescent in height, habit, and deciduous character of lower leaves, with distinct inflorescence axis, little or no branching of lateral elements of inflorescence, and throat cup of corolla abruptly expanded. *N. tomentosa* is highly polymorphic, *N. otophora* and *N. tomentosiformis* less so. *N. tomentosiformis* has closest affinity with *N. tomentosa*, but in inflorescence and calyx approaches *N. otophora*. *N. setchellii* is practically identical with the three species just named in leaf character, rather similar in habit and inflorescence, least similar in more bell-like flower. *N. glutinosa*, annual to limited perennial, exhibits the flower type of the first three species but differs in more raceme-like inflorescence, petioled leaf with blade cordate. A specialized floral type prevails throughout, the four species combining it with woodiness and large leaves. The distribution is exclusively Andean except for *N. glutinosa*, which ranges from northern coastal to southern Andean Peru. *N. setchellii* is restricted to northern Peru; *N. tomentosa* is found from north-central Peru to western Bolivia, *N. tomentosiformis* in western Bolivia, *N. otophora* in *yungas* of central Bolivia and subtropical northwestern Argentina. *N. glutinosa* alone is characteristic of arid areas. Habitat of other species, temperate to semitropical, rarely marginal in the *ceja de la montaña*. Chromosome number, 12 pairs.

Section GENUINAE Goodspeed, sect. nov.

Herbae, caule crasso; foliis decurrentibus, ovato-lanceolatis, sessilibus v. petiolatis; panicula multo-ramosa, patente aut compacta; corolla regulari, hypocrateriformi, vulgo longiore quam latiore, fauce superne gradatim v. abrupte inflata, limbo albo v. rubro, leviter v. profunde lobato; staminibus vulgo paulum inaequalibus, inclusis v. parum exsertis, infra medium corollae aequaliter affixis. Typus: *Nicotiana tabacum* L.

Thick-stemmed herbs; leaves decurrent, ovate-lanceolate, sessile to petiolate; panicle complexly branched, spreading or compact; corolla regular, salverform, usually longer than broad, throat gradually or abruptly inflated above, limb white to red, scarcely to deeply lobed; stamens usually somewhat unequal, included or slightly exserted, equally inserted below middle of corolla. Type: *N. tabacum* L.

The single species, *N. tabacum*, is a highly polymorphic, amphidiploid hybrid of a member of the section *Tomentosae* and *N. sylvestris* (section *Alatae*), or their progenitors. Inflorescence and flower blend those of both parental species, but extreme throat expansion links *N. tabacum* with section *Tomentosae* rather than with section *Alatae*. Contrasted with the perennial habit of most of section *Tomentosae*, *N. tabacum* is essentially annual but may persist longer in a depauperate condition. Certain *gigas* varieties exhibit short-day blooming tendency of many *Tomentosae*. Its occurrence is associated with some evidence of civilization (cf. *N. rustica*). As an escape, it is found throughout the geographical range of section *Tomentosae* and of *N. sylvestris*. Like *N. rustica*, it was introduced by pre- or post-Columbian man in North America and elsewhere. Chromosome number, 24 pairs.

Subgenus ***Petunioides*** (Don) Goodspeed, stat. nov.

Section *Petunioides* Don, Gen. Syst. 4, p. 465

Type: *Nicotiana acuminata* (Grah.) Hook.

Commonly herbs, usually rosette-forming; leaves petioled or sessile; flowers scattered, racemose, paniculate or distinctly cymose; corolla regular to somewhat zygomorphic, salverform or tubular-salverform, the limb whitish, slightly or deeply lobed, commonly vespertine.

Section UNDULATAE Goodspeed, sect. nov.

Herbae aut frutices vitae breves; foliis petiolatis; inflorescentia paniculata; corolla zygomorpha v. subregulari, hypocrateriformi, latitudine et longitudine vulgo aequali, limbo albo aut sordido; staminibus aequalibus, infra medium corollae aequaliter affixis aut uno breviore et aliquando inferiore quam alteris affixo. Typus: *Nicotiana undulata* R. & P.

Herbs or short-lived shrubs; leaves petioled; inflorescence paniculate; corolla zygomorphic or nearly regular, salverform, commonly equal in width and length, limb white or sordid; stamens equal and equally inserted below middle of corolla or one stamen shorter and sometimes lower in insertion. Type: *N. undulata* R. & P. Other members: *N. wigandioides* Koch & Fint., *N. arentsii* Goodsp.

N. undulata and *N. wigandioides* are related primarily by similarities in flower structure and by certain leaf characters. *N. undulata* shows elements in common with section *Paniculatae* and, to less degree, with *N. bonariensis*, section *Alatae*. *N. wigandioides* combines vegetative characters peculiar to section *Tomentosae* with flower similar to that of *N. bonariensis*. *N. arentsii* is a naturally occurring amphidiploid of the two other species of this section (or progenitors), presenting their morphological characters in blended condition. In distribution, *N. undulata* is Andean from somewhat north of central Peru, through Bolivia, into northwestern Argentina and northeastern Chile; *N. wigandioides*, in central and western Bolivia; *N. arentsii*, in southeastern Peru and adjacent western Bolivia. The first is subalpine; the second and third, subtropical or nearly so. Chromosome number, 12 pairs, except *N. arentsii*, 24 pairs.

Section TRIGONOPHYLLAE Goodspeed, sect. nov.

Herbae; foliis spathulatis v. sessili-trigonis; inflorescentia falso racemosa aut laxe ramosa; corolla tubuloso-hypocrateriformi, longiore quam latiore, limbo albido, vix v. clare lobato; staminibus inclusis v. subinclusis, uno quam alteris breviore, ad v. infra medium corollae aequaliter affixis. Typus: *Nicotiana trigonophylla* Dun.

Herbs; leaves spatulate to sessile-trigonate; inflorescence falsely racemose or loosely branching; corolla tubular-salverform, longer than broad, limb whitish, scarcely or distinctly lobed; stamens included or nearly so, one shorter, equally inserted at or below middle of corolla. Type: *N. trigonophylla* Dun. Other member: *N. palmeri* Gray.

The two species are closely related in all characters. In floral pattern they approach that of section *Paniculatae*, but otherwise are unrelated to members of the two other subgenera. *N. trigonophylla* is widely distributed in arid to semiarid Mexico and southernmost deserts of the western United States. *N. palmeri* occurs in a limited area of the southwestern United States. Chromosome number, 12 pairs.

Section ALATAE Goodspeed, sect. nov.

Herbae; foliis caulinis vulgo sessilibus, foliis basilaribus rosulatis, oblanceolato-spathulatis; inflorescentia falso racemosa, paniculata vel conspicue cymosa; corolla vulgo hypocrateriformi, longiore quam latiore, limbo vulgo albo, profunde lobato, fere semper vespertino; staminibus inclusis v. subinclusis, saepe inaequalibus, filamentis aliquando obsoletis, infime v. prope medium v. alte ad corollam aequaliter v. inaequaliter affixis. Typus: *Nicotiana alata* Link & Otto.

Herbs; cauline leaves usually sessile, the basal leaves rosulate, oblanceolate-spatulate; inflorescence falsely racemose, paniculate, or conspicuously cymose; corolla commonly salverform, longer than broad; limb generally white, deeply lobed, and nearly always vespertine; stamens included or nearly so, often unequal in length, the filaments sometimes obsolete, equally or unequally inserted low, near middle or high on corolla. Type: *N. alata* Link & Otto. Other members: *N. langsdorffii* Weinm. apud Roem. & Schult., *N. bonariensis* Lehm., *N. longiflora* Cav., *N. plumbaginifolia* Viv., *N. sylvestris* Speg. & Comes, *N. repanda* Willd., *N. stocktonii* Brandeg., *N. nesophila* Johnst.

The nine species are divisible into four morphological types. The first type includes *N. alata*, *N. bonariensis*, *N. longiflora*, and *N. plumbaginifolia*. The latter two species are closely related morphologically, with *N. bonariensis* approximating their habit and leaf but approaching *N. alata* in flower. In this type the corolla limb is vespertine, generally deeply lobed with ovate-acute segments; the inflorescence is subracemose or loosely branched. *N. langsdorffii*, the second type, resembles *N. alata* vegetatively but differs from other members of section in green, erect-limbed, nonvespertine flower. *N. sylvestris*, the third type, is somewhat distinct in many characters. In leaf, stoutness of stem, and nonvespertine flower it approximates species of the subgenus *Tabacum*; otherwise, basic characters of section *Alatae* predominate. The species of the fourth type, *N. repanda*, *N. stocktonii*, and *N. nesophila*, all are of amphidiploid origin, probably common on the basis of morphological similarities (cf. Goodspeed, 1945). These three species depart conspicuously in their tendency to combine decurrency of leaf blade with abruptly distinct petiole. *N. alata*, *N. bonariensis*, *N. langsdorffii*, and *N. longiflora*[1] are found in southeastern Brazil and adjacent regions to the south or west; *N. plumbaginifolia* is known from northern Argentina, in scattered localities in Bolivia, Peru, and Ecuador and in Guatemala, Mexico, and Cuba. *N. sylvestris* is characteristic of a narrow north–south strip in northwestern Argentina. *N. repanda*, *N. stocktonii*, and *N. nesophila* are North American; the first occurs in northeastern Mexico and adjoining Texas, and the latter two are peculiar to the Revillagigedo Islands. Chromosome number: *N. alata*, *N. bonariensis*, *N. langsdorffii*, 9 pairs; *N. longiflora* and *N. plumbaginifolia*, 10 pairs; *N. sylvestris*, 12 pairs; remaining species, 24 pairs.

Section NOCTIFLORAE Goodspeed, sect. nov.

Herbae; foliis brevi-petiolatis v. sessilibus, vulgo plus minusve linearibus; floribus solitariis, falso racemosis v. in paniculis semel-compositis; corolla hypocrateriformi, regulari, semel v. duplo longiore quam latiore, limbo albo, parum leviter lobato, vulgo vespertino; staminibus inclusis, longitudine inaequalibus, prope v. infra medium corollae aequaliter affixis. Typus: *Nicotiana noctiflora* Hook.

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[1] Also occurs as an introduction on or near the eastern and southeastern coast of the United States.

Herbs; leaves short-petioled to sessile, usually more or less linear; flowers solitary, falsely racemose, or in once compound panicles; corolla salverform, regular, once to twice as long as broad, limb white, rather shallowly lobed, usually vespertine; stamens unequal in length, included, equally inserted near or below middle of corolla. Type: *N. noctiflora* Hook.[2] Other members: *N. petunioides* (Griseb.) Millán, *N. ameghinoi* Speg., *N. acaulis* Speg.

The species are united by similarity in flower and leaf. In the most extreme species, *N. acaulis*, the stem is reduced to a peg bearing rosulate leaves and flowers just above the soil level; by vigorous root sprouting individual plants become carpets of rosettes. All the species are characteristic of dry regions of Argentina from the high Andes in the northwest, through the central portion, to the Patagonian desert, with a few marginal localities touching Chile. Distribution: *N. petunioides*, from northern border to Golfo San Jorge; *N. noctiflora*, more central (Tucuman to Rio Negro); *N. acaulis* and *N. ameghinoi*, in Chubut and Santa Cruz territories. Chromosome number, 12 pairs, except *N. ameghinoi*, of which the chromosome number is unknown.

Section ACUMINATAE Goodspeed, sect. nov.

Herbae annuae; foliis petiolatis v. sessilibus, caulinis vulgo lanceolatis; floribus solitariis aut in inflorescentibus falso racemosis, laxe paniculatis v. glomeratis; corolla regulari v. subzygomorpha, hypocrateriformi, minus duplo longiore quam latiore, limbo albo v. albido, leviter v. profunde lobato, vulgo vespertino; staminibus inaequalibus, inclusis v. parum exsertis, vulgo prope v. infra medium corollae aequaliter v. inaequaliter affixis. Typus: *Nicotiana acuminata* (Grah.) Hook.

Annual herbs; leaves petioled or sessile, cauline usually lanceolate; flowers solitary or in falsely racemose, loosely paniculate or glomerate inflorescences; corolla regular or somewhat zygomorphic, salverform, less than twice as long as broad, limb white or whitish, shallowly or strongly lobed, nearly always vespertine; stamens unequal, included or slightly exserted, equally or unequally inserted usually near or below middle of corolla. Type: *N. acuminata* (Grah.) Hook. Other members: *N. attenuata* Torr., *N. corymbosa* Remy, *N. pauciflora* Remy,[3] *N. miersii* Remy, *N. linearis* Phil., *N. spegazzinii* Millán, *N. bigelovii* (Torr.) Wats., *N. clevelandii* Gray, *N. nudicaulis* Wats.

All the species are strictly annual; they commonly form distinct, persistent rosettes, the first flowers in some species being borne near soil level. Except *N. nudicaulis*, all are vespertine, and, except *N. bigelovii*, are otherwise closely related morphologically. Size of plant and inflorescence are the most variable characters. The most closely related species pairs are: *N. acuminata* and *N. pauciflora*, *N. corymbosa* and *N. linearis*. *N. bigelovii* conforms in habit and leaf to sectional mode, in flower is reminiscent of *N. longiflora*, section *Alatae*. *N. nudicaulis*, *N. bigelovii*, and *N. clevelandii* are of amphidiploid origin, one parent in each case being a progenitor of members of section *Acuminatae* (cf. Goodspeed, 1945). The center of distribution is arid to semiarid northern and north-central Chile. *N. acuminata*,[4] *N. corymbosa*, *N. linearis*, and *N. miersii* occur also in western or southern Argentina. *N. spegazzinii* is peculiar to western Argentina, central and southern. *N. bigelovii* and *N. clevelandii* are confined, or nearly so, to arid and semiarid regions of the western United States, *N. nudicaulis* to similar terrain in northeastern Mexico. Chromosome number, 12 pairs, except three last-named species, 24 pairs.

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[2] It appears necessary with the evidence at present available to replace *N. cavanillesii* Dun. by *N. noctiflora* Hook. and *N. pampasana* O. Kuntze by *N. petunioides* (Griseb.) Millán.

[3] Priority of publication necessitates the replacement of *N. caudigera* Phil. by *N. pauciflora* Remy. The validity of *N. frigida* Phil., closely allied to members of this section, is not clear and this species is therefore not included here.

[4] Introduced on west coast of the United States.

Section SUAVEOLENTES Goodspeed, sect. nov.

Herbae; foliis basilaribus rosulatis, spathulatis v. oblanceolatis, foliis caulinis vulgo sessilibus v. alato-petiolatis; floribus vulgo falso racemosis v. late paniculatis; corolla paulum irregulari, hypocrateriformi, 1-3-plo longiore quam latiore, limbo albo, leviter v. parum profunde lobato, vulgo vespertino; staminibus inclusis v. subinclusis, inaequalibus, quatuor super medium corollae aequaliter v. inaequaliter affixis, uno breviore, parte longiore filamenti libera. Typus: *Nicotiana suaveolens* Lehm.

Herbs; lower leaves rosulate, spatulate or oblanceolate, cauline usually sessile or with winged petiole; flowers commonly falsely racemose or loosely paniculate; corolla slightly irregular, salverform, one to three times as long as broad, limb white, shallowly to rather strongly lobed, nearly always vespertine; stamens included or nearly so, unequal, four equally or unequally inserted in upper half of corolla, one shorter, a longer portion of its filament free. Type: *N. suaveolens* Lehm. Other members: *N. maritima* Wheeler, *N. velutina* Wheeler, *N. exigua* Wheeler, *N. gossei* Domin, *N. excelsior* Black, *N. benthamiana* Domin, *N. megalosiphon* Heurck & Müll. Arg., *N. goodspeedii* Wheeler, *N. occidentalis* Wheeler, *N. rotundifolia* Lindl., *N. debneyi* Domin, *N. fragrans* Hook., *N. ingulba* Black, *N. stenocarpa* Wheeler.

This is a well-integrated, geographically isolated group of species, closely similar in habit, inflorescence, and flower. All species, except *N. fragrans*, are annuals. *N. benthamiana* is the most isolated morphologically, in scattering of flowers along leafy stem and in cordate to broadly ovate character of the often petioled cauline leaves. The section shows certain relationships to American sections *Alatae*, *Noctiflorae*, and *Acuminatae*. *N. fragrans* is insular in the South Pacific; *N. debneyi* occurs on the east coast of Australia and is insular eastward to New Caledonia. The remaining species cover a large part of the Australian continent except desert and tropical regions. Characteristic habitat, arid to semiarid, interior or coastal. Known chromosome numbers: *N. suaveolens*, *N. maritima*, *N. velutina*, and *N. exigua*, 16 pairs; *N. gossei*, 18 pairs; *N. excelsior* and *N. benthamiana*, 19 pairs; *N. megalosiphon* and *N. goodspeedii*, 20 pairs; *N. occidentalis*, 21 pairs; *N. rotundifolia*, 22 pairs; *N. debneyi* and *N. fragrans*, 24 pairs.

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CHROMOSOME NUMBER AND MORPHOLOGY IN NICOTIANA

VII. KARYOTYPES OF FIFTY-FIVE SPECIES IN RELATION TO A TAXONOMIC REVISION OF THE GENUS

BY

T. H. GOODSPEED

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IN THE University of California Botanical Garden all but three of the fifty-eight species recognized in a recent taxonomic revision of the genus *Nicotiana* (Goodspeed, 1945*a*) are being grown. Some twenty-four new or little-known species in this collection represent products of three botanical expeditions to temperate South America and of the assistance of a number of local collectors there and in Australia and the South Pacific. Chromosome number and morphology of some of the fifty-five species have been reported as a contribution to an analysis of species origins and relationships (Goodspeed, 1933; 1934). To this same end, meiotic chromosome behavior in one hundred and thirty-one F_1 interspecific hybrids of *Nicotiana* has been analyzed, together with detailed determination of the comparative morphology and the distribution of the majority of species.

The taxonomic revision of *Nicotiana* referred to above involves the recognition of three subgenera (*Rustica*, *Tabacum*, and *Petunioides*) and a series of sections under each subgenus. This taxonomic organization is based primarily upon morphological and distributional evidence, although knowledge of chromosome number, morphology, and behavior in interspecific hybrids influenced to some extent the character of the arrangement with respect to certain species and groups of species. Morphological and distributional evidence referred to briefly in what follows is given in more detail in the article dealing with the taxonomic aspect (Goodspeed, 1945*a*). Incidental reference will here be made to the extent and character of conjugation at MI in F_1 interspecific hybrids; somewhat more detailed information in this connection is given elsewhere (Goodspeed, 1945*b*; Wheeler, 1945), and complete treatment of this subject is in preparation. Similarly, additional general cytological information on the genus is referred to in a forthcoming article (Goodspeed, 1945*b*) and will be fully commented upon and documented in a subsequent publication.

In the present article, following a general consideration of chromosome number and chromosome morphology in *Nicotiana*, the karyotypes of fifty-five of the fifty-eight recognized species are tabulated and, under subgeneric and sectional headings, are discussed and illustrated.* The term karyotype is employed here to refer to the sum total of the physical properties of the chromosomes of a complement visible at somatic metaphase (cf. Levitsky, 1924).

CHROMOSOME NUMBER

In more than half of some two hundred and fifty Solanaceous species for which chromosome number is known, 12 pairs or multiples thereof occur. Other chromosome numbers reported in the *Solanaceae* are 7, *ca.* 8, 9, 10, 11, 14, 16, 17, 18, 19, 20, 21, 22, 30, and 34. The *Scrophulariaceae* show a similar wide range of chromosome numbers—6, 7, 8, 9, 10, 12, 14, 15, 16, 17, 20, 23, 25, 26, 28, and 30—and for another related family, the *Nolanaceae*, the three species investigated all show 12 pairs. Chromosome numbers in some genera of the *Solanaceae* related to *Nicotiana* are: *Petunia*, 7 or 9 pairs; *Fabiana* and *Nierembergia*, 9 pairs; and *Salpiglossis*, 22 pairs (cf. Goodspeed, 1933). Of these genera, *Petunia* probably stands closest to *Nicotiana* morphologically, and the occurrence of 7 pairs in the former has been referred to (Kostoff, 1943) as indicating a basic 6 pairs in the latter. The presence of 9-paired species in both genera is to be noted.

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* Chromosome number and morphology of *N. ameghinoi*, *N. stenocarpa*, and *N. ingulba* are unknown.

TABLE 1

Chromosome Numbers (Haploid) of Fifty-Five Species of Nicotiana

N. acaulis	12	Goodspeed, 1945a*
N. acuminata	12	Goodspeed, 1923
N. alata	9	Goodspeed, 1924
N. arentsii	24	Goodspeed, 1944
N. attenuata	12	Clausen, 1928
N. benavidesii	12	Goodspeed, 1938
N. benthamiana	19	Wheeler, 1945
N. bigelovii	24	Goodspeed, 1923
N. bonariensis	9	Clausen, 1932
N. clevelandii	24	Clausen, 1928
N. cordifolia	12	Clausen, 1928
N. corymbosa	12	Goodspeed, 1933
N. debneyi	24	Goodspeed, 1933 (from Wheeler)
N. excelsior	19	Wheeler, 1945
N. exigua	16	Kostoff, Dogadkina, and Tichenova, 1935
N. fragrans	24	Wheeler, 1945
N. glauca	12	Goodspeed, 1923
N. glutinosa	12	Goodspeed, 1923
N. goodspeedii	20	Goodspeed, 1934 (from Wheeler)
N. gossei	18	Wheeler, 1935
N. knightiana	12	Goodspeed, 1938
N. langsdorffii	9	Goodspeed, 1923
N. linearis	12	Goodspeed, 1945a
N. longiflora	10	Goodspeed, 1923
N. maritima	16	Wheeler, 1935
N. megalosiphon	20	Goodspeed, 1933 (from Wheeler)
N. miersii	12	Goodspeed, 1933
N. nesophila	24	Goodspeed, 1933
N. noctiflora†	12	Clausen, 1932
N. nudicaulis	24	Goodspeed, 1923
N. occidentalis	21	Wheeler, 1945
N. otophora	12	Goodspeed, 1945a
N. palmeri	12	Christoff, 1928
N. paniculata	12	Goodspeed, 1923
N. pauciflora†	12	Goodspeed, 1923
✓ N. petunioides†	12	Goodspeed, 1933
✓ N. plumbaginifolia	10	Christoff, 1928
N. raimondii	12	Goodspeed, 1933
N. repanda	24	Clausen, 1928
N. rotundifolia	22	Goodspeed, 1933 (from Wheeler)
✓ N. rustica	24	East, 1921
N. sanderae	9	Malloch and Malloch, 1925
N. setchellii	12	Goodspeed, 1941
N. solanifolia	12	Clausen, 1928
N. stocktonii	24	Clausen, 1932
N. suaveolens	16	Goodspeed and Clausen, 1927a
	32	East, 1928 (from Goodspeed)
N. sylvestris	12	Goodspeed, 1923
N. tabacum	24	White, 1913
N. thyrsiflora	12	Goodspeed, 1945a
N. tomentosa	12	Goodspeed and Clausen, 1927b
N. tomentosiformis†	12	Brieger, 1928
N. trigonophylla	12	Clausen, 1928
N. undulata	12	Clausen, 1932
N. velutina	16	Wheeler, 1935
N. wigandioides	12	Clausen, 1932

* References are to author who first reported the valid chromosome number of the species.

† The chromosome numbers of *N. noctiflora*, *N. pauciflora*, *N. petunioides*, and *N. tomentosiformis* were previously referred to by the author under the designations *N. cavanillesii*, *N. caudigera*, *N. pampasana*, and *N. rusbyi*, respectively.

In the genus *Nicotiana*, as in the *Solanaceae* as a whole, 12 pairs or a multiple of 12 is characteristic of at least half the species, while the rest show a range in number which is wider than is usual within a single genus of the *Solanaceae*. As shown in table 1, of fifty-five species for which chromosome number is known, twenty-eight show 12 pairs, eleven show 24 pairs, four 16 pairs, three 9 pairs, two 10, 19, or 20 pairs, and one each shows 18, 21, or 22 pairs. Of the eleven 24-paired species all the nine American ones appear to be of amphidiploid origin (Goodspeed and Bradley, 1942), progenitors of two of the 12-paired species being involved in each.

The polymorphism of certain species of *Nicotiana* has long been known, and a considerable number of varieties of such species as *N. tabacum*, *N. rustica*, *N. bigelovii*, and *N. longiflora* have been described or otherwise recognized. The author's studies of herbarium material and particularly of cultures grown from seed collected in the wild have shown that the majority of *Nicotiana* species exhibit an equivalent, or at least a considerable degree of, polymorphism. Chromosome number has been determined not only for most of the recognized varieties of the classical species, but also for a series of previously unknown varieties or forms of each of a large number of other species. Since the named as well as the unnamed varieties of the species listed in table 1 show the same chromosome number as the species itself, only the latter is reported here.

The majority of the chromosome numbers referred to in table 1 were originally determined from studies of MI and MII in PMC or, in some species, of root-tip mitoses, or, less frequently, of both. Recently, chromosome number in fifty of the fifty-five species listed in table 1 has been redetermined by studies of first microspore mitoses in temporary acetocarmine smears. For three species—*N. acaulis*, *N. petunioides*, and *N. thyrsiflora*—root-tip mitoses alone were available.

CHROMOSOME MORPHOLOGY

Evidence concerning chromosome morphology in the majority of the species of *Nicotiana* has hitherto been fragmentary, or at most general, except in certain members of section *Alatae* (Avery, 1938; Goodspeed and Avery, 1939) and in thirteen Australian-South Pacific species studied by Wheeler (1945). That which follows is complete and detailed for all but a few of the fifty-eight species and is based upon analysis of first microspore mitoses supplemented by comparative studies of root-tip mitoses.

The chromosomes of *Nicotiana* species are relatively small to medium, varying in the several genoms from *ca.* 2 μ to somewhat more than 5.5 μ in average length. In spite of considerable size variation from tissue to tissue or between different mid-phases of mitosis, there are in *Nicotiana* consistent and appreciable size distinctions within certain genoms and between genoms, the significance of which will be referred to below.

In addition to distinctions in size, those involving position of the centromere, number and types of satellited pairs, size and position of satellites, and occurrence of additional constrictions characterize the chromosomes of the different genoms. Position of the centromere is reflected in difference in brachial ratios and chromosomes are, in the karyotype formulae (cf. table 2) referred to as median (*m*), submedian (*sm*) or subterminal (*st*) where this ratio (length of long arm vs. that of short arm) is respectively 1 : 1, greater than 1 : 1 but less than 3 : 1, and 3 : 1 or greater. In most of the subterminal chromosomes in *Nicotiana* the arm ratio is definitely greater than 3 : 1, and in many, but not consistently, the short arm

TABLE 2

KARYOTYPES OF FIFTY-FIVE SPECIES OF NICOTIANA

	Number of pairs	*m*	*sm*	*st*	Fig.
Subgenus Rustica					
Section Paniculatae					
N. glauca	12	1	1	10^{1*}	1, *a*
N. raimondii	12	4	8^1		1, *b*
N. solanifolia	12	4	8^1		1, *c*
N. cordifolia	12	4	8^1		1, *d*
N. benavidesii	12	6	4^1	2^1	1, *e*
N. knightiana	12	6	6^1		1, *f*
N. paniculata	12	6	6^1		1, *g*
Section Thyrsiflorae					
N. thyrsiflora	12	12^1			1, *h*
Section Rusticae					
N. rustica	24	12	12^2		1, *i*
Subgenus Tabacum					
Section Tomentosae					
N. tomentosiformis	12	7^1		5^1	2, *a*
N. otophora	12	7^1		5^1	2, *b*
N. tomentosa	12	3^1	4	5^1	2, *c*
N. setchellii	12	7^1	5		2, *d*
N. glutinosa	12	5	7^1		2, *e*
Section Genuinae					
N. tabacum	24	10^1	5^1	9^1	2, *f*
Subgenus Petunioides					
Section Undulatae					
N. wigandioides	12	5	3	4^1	3, *a*
N. undulata	12	6	6^1		3, *b*
N. arentsii	24	11	9^1	4^1	3, *c*
Section Trigonophyllae					
N. trigonophylla	12	4	5	3^1	4
N. palmeri	12	4	5	3^1	
Section Alatae					
N. alata	9	4	2	3^2	5, *a*
N. langsdorffii	9	2	4^1	3^1	5, *b*
N. bonariensis	9	2	3	4^2	5, *c*
N. longiflora	10			10^2	5, *d*
N. plumbaginifolia	10			10^2	5, *e*
N. sylvestris	12	3	5^1	4^1	5, *f*
N. repanda	24	10	8	6^3	5, *g*
N. stocktonii	24	10	11^1	3^1	5, *h*
N. nesophila	24	10	11^1	3^1	5, *i*

* Superscript numbers refer to occurrence of satellites on chromosomes of the morphological type in question.

TABLE 2 (*Continued*)

	Number of pairs	*m*	*sm*	*st*	Fig.
Section Noctiflorae					
N. acaulis	12			12^{2}	6, *a*
N. noctiflora	12			12^{3}	6, *b*
N. petunioides	12		1	11^{2}	6, *c*
Section Acuminatae					
N. attenuata	12	2	6^{1}	4^{1}	7, *a*
N. corymbosa	12	2	6^{1}	4^{1}	7, *b*
N. acuminata	12	2	6^{1}	4^{1}	7, *c*
N. pauciflora	12	2	6^{1}	4^{1}	
N. miersii	12	2	6^{1}	4^{1}	7, *d*
N. spegazzinii	12	1	3^{1}	8^{1}	7, *e*
N. linearis	12	1	3^{1}	8^{1}	7, *f*
N. bigelovii	24	8	10^{1}	6^{1}	7, *g*
N. clevelandii	24	8	$10^{1?}$	$6^{1?}$	7, *h*
N. nudicaulis	24	5	12	7^{1}	7, *i*
Section Suaveolentes†					
N. suaveolens	16	8^{1}	4^{1}	4	
N. maritima	16	8^{1}	4^{1}	4	
N. velutina	16	8^{1}	4	4^{1}	
N. exigua	16	6^{1}	5	5^{1}	
N. gossei	18	5	4^{1}	9^{1}	
N. excelsior	19	5	4^{1}	10^{1}	
N. benthamiana	19	1	$4^{1?}$	14^{1}	
N. megalosiphon	20	2	4^{1}	14^{1}	
N. goodspeedii	20	6^{1}	4^{1}	10	
N. occidentalis	21	4	3	14^{1}	
N. rotundifolia	22	4^{1}	3	15^{1}	
N. debneyi	24	4^{1}	1	19^{1}	
N. fragrans	24	2^{1}	6	$16^{2?}$	

† The karyotypes of this section are quoted from Wheeler (1945).

appears as a spherical "head" (cf. "knob chromosomes," Babcock and Jenkins, 1943; "headed chromosomes," Levitsky, 1931). In certain chromosomes (cf. *N. longiflora*, p. 358) the short arm is so reduced that the position of the centromere is at times not distinguishable. In the genus as a whole, median and submedian chromosomes predominate over subterminal ones in the ratio of approximately 5 : 3, each of the three subgenera showing the following distinctive ratios: subgenus *Rustica*, 9 : 1; subgenus *Tabacum*, 5 : 2; and subgenus *Petunioides*, 4 : 3.

In *Nicotiana* the genom of every species includes at least one pair of satellited chromosomes. Frequently two pairs, and in some species three, especially those of higher chromosome number, bear satellites. Satellites vary in size of chromosome segment and in length of thread separating the segment from the body of the chromosome, although these distinctions are relatively constant for the same chromosome pair. In species where only one pair of chromosomes is satellited, it is usually a subterminal pair if there is such in the genom; if two or more pairs bear satellites, the second and third may be either submedian or subterminal, but rarely median chromosomes (cf. however, section *Tomentosae*). Usually the satellites are proximal (on the short arm), exceptions being noted in what follows.

In many species of *Nicotiana*, both in the American (Sarana, 1934; Goodspeed, 1934; Avery, 1938; Goodspeed and Avery, 1939) and particularly in the Australian-South Pacific species (Wheeler, 1945), there have been observed more or less distinct constrictions in addition to those indicating position of centromere and to those known to be associated with satellites. They are usually near the ends of the longer arms of submedian chromosomes, although they may occur on the longer arms of subterminal or on one or both arms of median chromosomes, and their presence is frequently indicated by flexure of the chromosome arm at the point of constriction.

Table 2 (pp. 348–349) contains the karyotype formulae of fifty-five species of *Nicotiana* arranged according to a taxonomic revision of the genus (Goodspeed, 1945*a*). The species of the same chromosome number are listed within each section according to decreasing average size of the chromosomes which make up their genoms.

In what follows, the species karyotypes contained in table 2 are illustrated and discussed under their respective subgenera and sections. With few exceptions the illustrations represent the chromosomes of a single metaphase plate of a first microspore mitosis. Figures 1 and 2 include the species of subgenus *Rustica* and subgenus *Tabacum*, respectively, while the sections of subgenus *Petunioides* (except section *Suaveolentes*, cf. p. 362) are represented each by a separate figure (3–7). The karyotypes of each section are arranged according to decreasing average size of chromosomes. Within each species the median chromosomes are shown first, next the submedian, and last the subterminal, in sequence of decreasing size within each morphological category. All figures are × 2,250.

SUBGENUS RUSTICA

Of the nine species of this subgenus (cf. Goodspeed, 1945*a*) eight are illustrated as to karyotypes in figure 1. That of *N. thyrsiflora*, section *Thyrsiflorae*, is not included because equivalent evidence from first pollen grain mitoses is not available. The karyotype formula (12^1 *m* or *sm*) of that species as reported in table 2 was determined from analyses of root-tip mitoses where no appreciable size differences within the genom appeared and the distinctions which doubtless obtain between median and submedian chromosomes were difficult to determine. Earlier characterizations of the karyotypes of *N. glauca, N. solanifolia, N. raimondii*, and *N. paniculata* (Goodspeed, 1934) are confirmed.

The detailed evidence presented in figure 1 shows that in section *Paniculatae*, apart from *N. glauca* (fig. 1, *a*), the average chromosome length of the remaining six species (fig. 1, *b–g*) is much the same in the first four but appreciably less in the last two, and that the karyotypes of these six species apart from two chromosomes of *N. benavidesii* (fig. 1, *e*) present a uniform pattern of median and submedian chromosomes, one submedian in each species being satellited. The relative number of median and submedian chromosomes varies from 4 median and 8 submedian in *N. solanifolia, N. raimondii*, and *N. cordifolia* to 6 median and 6 submedian in *N. knightiana* and *N. paniculata*. Of the six species, the karyotype of *N. benavidesii* alone contains subterminal chromosomes, one of them satellited. Intragenomic variation in size is limited, although it is to be noted that one of the median chromosomes in each genom is distinctly smaller than the remaining members of that morphological type. In addition, the satellited (submedian) chromosome in each species is identical in terms of size relative to that of the other chromosomes and thus appears throughout as No. 8 in a sequence based upon relative size within the genom. In *N. paniculata* the satellited submedian chromosome closely approaches the median in position of centromere. Throughout the section there is present near the end of the longer arm of a submedian pair of corresponding size (No. 10) in each genom an additional constriction, indicated usually by a flexure at its point of occurrence.

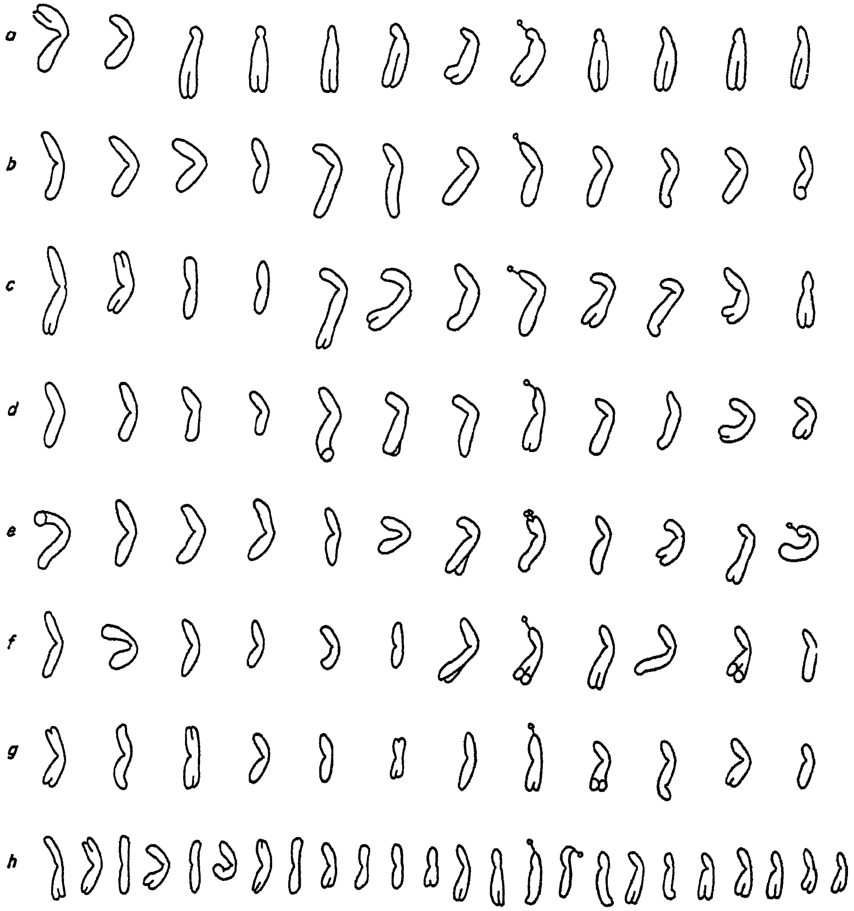

Fig. 1. Karyotypes of subgenus *Rustica*. *a*, *N. glauca* (1 *m* + 1 *sm* + 10^1 *st*). *b*. *N. raimondii* (4 *m* + 8^1 *sm*). *c*, *N. solanifolia* (4 *m* + 8^1 *sm*). *d*, *N. cordifolia* (4 *m* + 8^1 *sm*). *e*, *N. benavidesii* (6 *m* + 4^1 *sm* + 2^1 *st*). *f*, *N. knightiana* (6 *m* + 6^1 *sm*). *g*, *N. paniculata* (6 *m* + 6^1 *sm*). *h*, *N. rustica* (12 *m* + 12^2 *sm*).

The karyotype of *N. glauca* departs from the basic pattern in section *Paniculatae* since it consists primarily of subterminal chromosomes. Interpretation of the description by Sarana (1934; cf. also Kostoff, 1943) of the genom of *N. glauca* in general confirms an earlier one by the author (Goodspeed, 1934), except that the chromosome classified in the latter as submedian (fig. 1, *a*, No. 2) is apparently classified by Sarana as subterminal. However, the limited range of variation in length and arm ratio provides little basis for Sarana's and Kostoff's classification of the chromosomes of *N. glauca* under six or seven different morphological types. As shown in figure 1, the chromosomes of this species are large (cf. Christoff, 1928; Goodspeed, 1934; Sarana, 1934; Kostoff, 1943), but not outstandingly so either in subgenus *Rustica* or elsewhere in the genus; indeed, their total length is less than that of *N. acaulis* (cf. fig. 6, *a*).

Section *Rusticae* contains the single species *N. rustica*. An amphidiploid of two 12-paired species, its genom possesses 24 pairs. Except for that of Sarana (1934), whose description is somewhat definitive, earlier studies (Christoff, 1925; Rybin, 1927; Kostoff, 1935) comment only on the general morphological similarity of the chromosomes of *N. rustica*. In first pollen grain mitoses the karyotype of this species (fig. 1, *h*) has been determined to be $12\ m + 12^2\ sm$. Details of chromosome morphology include the occurrence of one median pair smaller than the remaining median pairs, of an otherwise gradual range in size, of two satellited submedian pairs, one of which approaches the median in position of centromere, and the presence of additional constrictions on the longer arms of one submedian pair.

Degrees of taxonomic relationship and details of distribution of the species of subgenus *Rustica* are given elsewhere (Goodspeed, 1945*a*). They indicate that this subgenus is in general a morphological unit and that sections *Paniculatae* and *Rusticae* are most similar and definitely distinguishable from section *Thyrsiflorae*. The species of section *Paniculatae* are, with the exception of *N. glauca*, clearly interrelated. The latter stands somewhat apart on the basis of certain morphological characters. In similarities and dissimilarities of detail, the karyotypes of the nine species of the subgenus *Rustica* largely correspond to the morphological-distributional picture. Thus, the two most closely related species, *N. paniculata* and *N. knightiana*, are practically indistinguishable in terms of karyotype. Similarly, relatively slight differences in karyotype characterize *N. solanifolia*, *N. raimondii*, *N. benavidesii*, and *N. cordifolia*. As already indicated, *N. glauca* differs karyologically from all other species of the subgenus. Although given sectional status because of certain morphological distinctions, *N. thyrsiflora* has a karyotype similar in basic pattern to that of section *Paniculatae*. Finally, in the karyotype of *N. rustica* elements of the karyotypes of the modern representatives of its amphidiploid ancestors (*N. paniculata* or other member of section *Paniculatae*, and *N. undulata*, cf. p. 354; fig. 3, *b*) can be recognized.

SUBGENUS TABACUM

The karyotypes of the six species of this subgenus for which formulae are given in table 2 are illustrated in figure 2, where the five 12-paired species of section *Tomentosae* are followed by the single 24-paired species of section *Genuinae*. Earlier analyses (Goodspeed, 1934) of *N. tomentosa* and *N. glutinosa* are confirmed, but the formula of *N. tomentosiformis*, previously reported as $9^1\ m$ or $sm + 3\ st$, is now known to be $7^1\ m + 5^1\ st$. Therefore, as shown in table 2 and in figure 2, the three species *N. tomentosiformis*, *N. otophora*, and *N. tomentosa* possess in common the karyotype pattern $7^1\ m$ or $sm + 5^1\ st$, in contrast to *N. setchellii* and *N. glutinosa*, which show $12^1\ m$ or sm. Of the first three, *N. tomentosiformis* and *N. otophora* are practically identical in karyotype, with a strikingly dimorphic complement of seven median and five subterminal chromosomes, the latter approximately three times the length of the former. Two minor distinctions have been observed. In *N. otophora* all the seven median pairs are exceedingly short, while in *N. tomentosiformis* one median pair is considerably longer than the rest and approaches in length the shortest of the subterminal pairs. In the latter species one of the subterminal pairs (No. 10), in contrast to the "headed" appearance of the remaining chromosomes of this category in both species, is distinct in being J-shaped with an arm ratio of approximately 3 : 1. The genom of *N. tomentosa*, with smaller average chromosome size than *N. tomentosiformis* and *N. otophora*, is less strikingly dimorphic than the genoms of the latter two species and is composed of $3^1\,m + 4\,sm + 5^1\,st$ pairs of chromosomes with less pronounced size distinctions. The genom of *N. tomentosa* is further characterized by the occurrence of constrictions in addition to those associated with centromere and with satellite on at least one pair of chromosomes of each morphological type.

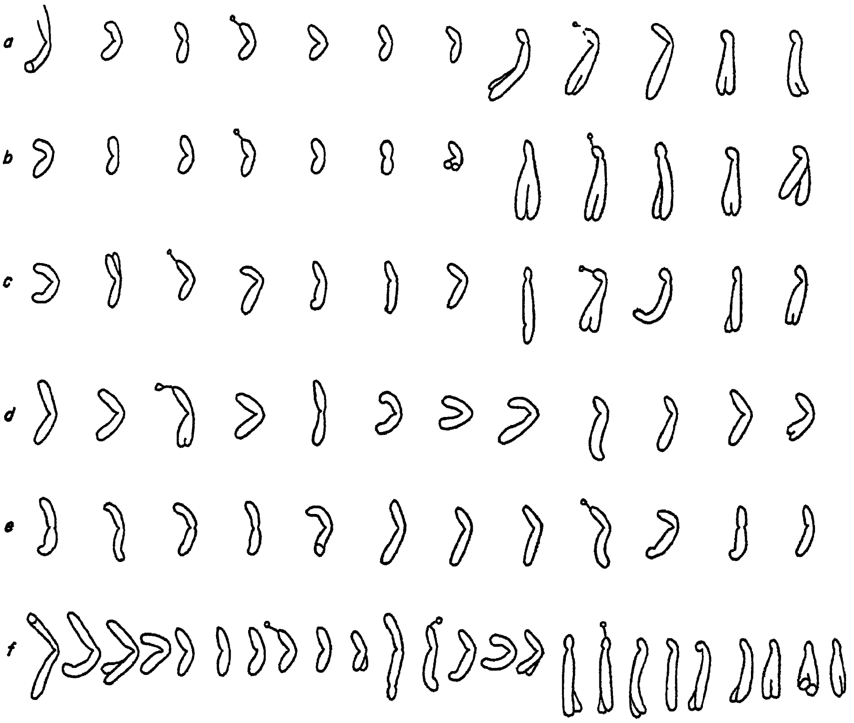

Fig. 2. Karyotypes of subgenus *Tabacum*. *a*, *N. tomentosiformis* ($7^1\,m + 5^1\,st$). *b*, *N. otophora* ($7^1\,m + 5^1\,st$). *c*, *N. tomentosa* ($3^1\,m + 4\,sm + 5^1\,st$). *d*, *N. setchellii* ($7^1\,m + 5\,sm$). *e*, *N. glutinosa* ($5\,m + 7^1\,sm$). *f*, *N. tabacum* ($10^1\,m + 5^1\,sm + 9^1\,st$).

The complements of *N. setchellii* and *N. glutinosa*, although similar in possessing all median or submedian chromosomes of relatively uniform size, show certain specific distinctions in chromosome morphology. The karyotype of *N. setchellii* is $7^1\,m + 5\,sm$, the satellite is larger than in any of the other species of this section, and in none of the subterminal chromosomes does the centromere approach the borderline between a submedian and subterminal position. By contrast, in *N. glutinosa*, with karyotype of 5 *m* + 7^1 *sm*, the centromere of at least three of the submedian pairs approaches this borderline—indeed, three pairs were classified as subterminal in an earlier, root-tip, analysis (Webber, 1933).

Like *N. rustica* of subgenus *Rustica*, *N. tabacum* (24 pairs) is of an amphidiploid origin (Goodspeed and Clausen, 1928; Goodspeed and Bradley, 1942; Clausen and Cameron, 1944) in which two 12-paired species are involved. Its karyotype has been variously described from root-tip analyses, and all earlier characterizations (Nikolajewa, 1924; Christoff, 1925; Ruttle, 1928; Rybin, 1927; Sarana, 1934) agree in emphasizing conspicuous distinctions both in chromosome size and in chromosome morphology within its complement, in contrast to the general uniformity in size and morphology of the chromosomes of *N. rustica*. These earlier, generalized descriptions are confirmed and amplified by recent studies of first pollen grain mitoses from which the formula 10^1 *m* + 5^1 *m* + 9^1 *st* is derived. Of the ten median pairs, three are longer and more sharply flexed than the remaining seven, one pair of the latter being satellited. Three submedian pairs, including the longest pair of this type with arms only slightly unequal in length and the satellited submedian pair, possess additional constrictions near the ends of the longer arms. The nine subterminal pairs show only small variation in length, the longest approximately equaling the longest median and submedian pairs.

Viewed as a whole, the karyotypes of the 12-paired species of subgenus *Tabacum* differ in general detail from those of subgenus *Rustica*. Thus, the dimorphism within the genom of each of the first three species of section *Tomentosae* listed in table 2 and the karyotype distinctions between these species and the remaining two species in that section produce a different picture from that of subgenus *Rustica*, in which, apart from *N. glauca*, the 12-paired species exhibit a decided uniformity in karyotype pattern. Taxonomically, *N. tomentosiformis*, *N. otophora*, and *N. tomentosa* appear to be closely related, the first and the last most conspicuously so. Karyologically also these three species form a unit, within which, however, the genom of *N. otophora* rather than that of *N. tomentosa* is practically identical with that of *N. tomentosiformis*. Of *N. glutinosa* and *N. setchellii* the karyotypes are similar, with a pattern distinct from that of the cluster of three species just referred to. On the other hand, both *N. glutinosa* and *N. setchellii* could taxonomically be more readily identified with those three species than with each other. As shown in figures 2 and 5 and by the pertinent formulae (table 2), the karyotype of *N. tabacum* displays in some detail a combination of the chromosomes characteristic of the cluster of three species of section *Tomentosae* and those characteristic of *N. sylvestris* (subgenus *Petunioides*, section *Alatae*, p. 358), species descended from those which were originally concerned in the amphidiploid origin of *N. tabacum*.

SUBGENUS PETUNIOIDES

Five of the six sections of this subgenus for which karyotype formulae are listed in table 2 are illustrated in figures 3 to 7. The sixth, section *Suaveolentes*, will be illustrated elsewhere by Dr. H-M. Wheeler. Since subgenus *Petunioides* is large and diversified, its various sections are separately discussed and illustrated in what follows.

Section *Undulatae*.—In section *Undulatae* there are two 12-paired species, *N. undulata* and *N. wigandioides*, and one 24-paired species, *N. arentsii*, the last an amphidiploid into the origin of which the two 12-paired species entered (Goodspeed, 1944). Earlier analyses of the karyotypes of *N. undulata* and *N. wigandioides* (Goodspeed, 1934) are here confirmed and amplified by the recognition of distinctions between median and submedian chromosomes. Thus, the earlier formula of *N. undulata*, 12^1 *m* or *sm*, now becomes 6 *m* + 6^1 *sm*, and that of *N. wigandioides*, 8 *m* or *sm* + 4^1 *st*, becomes 5 *m* + 3 *sm* + 4^1 *st*. The differences in length of chromosomes within each genom are not marked, but the total chromosome length in *N. undulata* is slightly less than that in *N. wigandioides*. In *N. arentsii* the karyotype, 11 *m* + 9^1 *sm* + 4^1 *st*, completely reflects the karyotypes of the two 12-paired species involved in its amphidiploid origin, for, as is shown in figure 3, the complement of *N. arentsii* is divisible into two subgenoms, one similar in chromosome morphology to the karyotype of *N. undulata* and the other to that of *N. wigandioides*. Although the chromosomes of *N. arentsii* are in general smaller than those of the two other species of this section, their size distinctions are well marked.

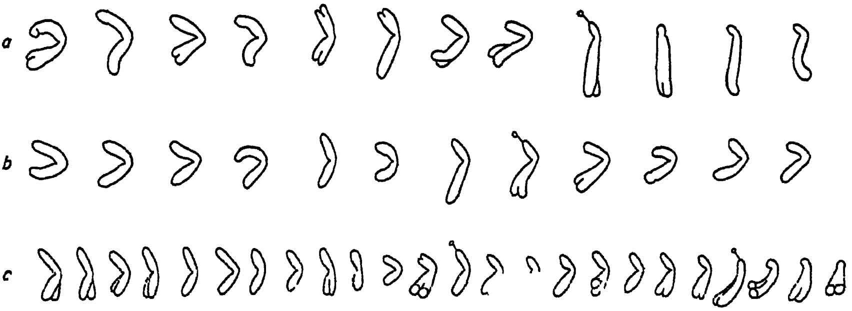

Fig. 3. Karyotypes of section *Undulatae*. *a*, *N. wigandioides* (5 *m* + 3 *sm* + 4^1 *st*). *b*, *N. undulata* (6 *m* + 6^1 *sm*). *c*, *N. arentsii* (11 *m* + 9^1 *sm* + 4^1 *st*).

Elsewhere it has been noted (Goodspeed, 1945*a*) that taxonomically section *Undulatae* represents somewhat of a transition between subgenus *Petunioides* and the two other subgenera. Thus, certain features characteristic of species of subgenus *Rustica* are present in *N. undulata*, and in *N. wigandioides* certain features which characterize species of subgenus *Tabacum*, while *N. arentsii* represents a combination of the morphological characters of the two species and its distribution appears to overlap theirs (Goodspeed, 1944). Evidence from chromosome morphology largely confirms these interpretations of relationship, for the similarity in karyotype between *N. undulata* and members of section *Paniculatae* (fig. 1) is obvious, the large subterminal chromosomes of *N. wigandioides* are reminiscent of elements of the genoms in section *Tomentosae* (fig. 2), and, finally, the genom of *N. arentsii* can be interpreted as the sum of the genoms of the two other members of section *Undulatae*.

Section *Trigonophyllae*.—Of the two 12-paired species of this section, *N. trigonophylla* and *N. palmeri*, the karyotype of the former is illustrated in figure 4. Since *N. palmeri* is taxonomically so closely related to *N. trigonophylla* that its claim to specific recognition is somewhat doubtful, it is probable that the karyotypes of the two species are indistinguishable. The author earlier reported (Goodspeed, 1934) the karyotype of *N. trigonophylla* as 9 *m* or *sm* + 3^1 *st*. In first pollen grain mitoses it is now possible to distinguish between median and submedian chromosomes and thus to derive the complete formula 4 *m* + 5 *sm* + 3^1 *st*. Earlier, the chromosomes of

N. trigonophylla were characterized as the smallest in the genus (Goodspeed, *l.c.*), but it is now known that those of two other 12-paired species, *N. linearis* and *N. spegazzinii*, and of 24-paired *N. nudicaulis*, all of which are members of section *Acuminatae*, are at least as small as those of *N. trigonophylla* (cf. fig. 7, *e*, *f*, and *i*). This and other similarities in chromosome morphology between *N. trigonophylla* and *N. nudicaulis*, together with evidence from distribution and external morphology (Goodspeed, 1945*a*), and from chromosome behavior in F_1 interspecific hybrids (Goodspeed, 1945*b*), contribute to the conclusion that a progenitor of *N. trigonophylla* represents one of the parents of the amphidiploid species *N. nudicaulis* (cf. also section *Acuminatae*).

Section *Alatae*.—Evidence from chromosome number and morphology divide this section into a 9-paired, a 10-paired, a 12-paired, and a 24-paired group of species. Taxonomically, a cluster composed of the 9-paired species *N. alata*,[*] *N. langsdorffii*, and *N. bonariensis*, and of 10-paired *N. longiflora* and *N. plumbaginifolia*, can be recognized, and the karyotypes of these five species exhibit essential similarities and also certain dissimilarities. Various earlier investigations (Ruttle, 1927; Goodspeed and Avery, 1929; Goodspeed, 1934; Avery, 1938) indicate a common basic karyotype of 5 *m* or *sm* + 4^2 *st* for the three 9-paired species and more specifically report: *N. alata*, 2 *m* (large) + 3 *m* or *sm* (small) + 4^2 *st*; *N. langsdorffii* and *N. bonariensis*, 1 *m* (large) + 1 *sm* (large) + 3 *m* or *sm* (small) + 4^2 *st*. Recent analyses confirm in general these earlier ones. However, with respect to the small chromosomes earlier classified as "*m* or *sm*" it has been possible to distinguish between these two categories, and centromere position for one subterminal pair in each of two species is reinterpreted. The formulae therefore become: *N. alata*, 4 *m* (2 large) + 2 *sm* (small) + 3^2 *st*; *N. langsdorffii*, 2 *m* (1 large) + 4^1 *sm* (1 large) + 3^1 *st*; *N. bonariensis*, 2 *m* (1 large) + 3 *sm* (1 large) + 4^2 *st*. In these more detailed karyotypes and in the corresponding illustrations of the three 9-paired species (fig. 5, *a*–*c*) it will be noted that of the two large pairs in each species both are median in *N. alata*, but that one is median and one submedian in *N. langsdorffii*[†] and in *N. bonariensis*. Of the three small chromosomes earlier classified as median or submedian it is now know that two are median and one submedian in *N. alata*, one median and two submedian in *N. langsdorffii* and *N. bonariensis*, and that one of the four chromosomes earlier classified as subterminal falls, in *N. alata* and in *N. langsdorffii*, into the submedian category. There are other significant details of chromosome morphology earlier reported in the 9-paired species and now confirmed. On each of the two large median pairs in *N. alata* and on the large median pair in *N. langsdorffii*, additional constrictions occur near the extremity of one arm, and with respect to at least one of these pairs in *N. alata* such constrictions may be

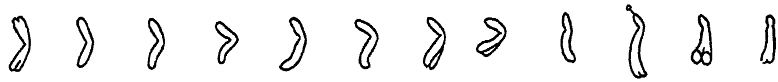

Fig. 4. Karyotype of section *Trigonophyllae*. *N. trigonophylla* (4 *m* + 5 *sm* + 3^1 *st*).

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[*] The karyotype of *N. sanderae*, a horticultural variety, is identical with that of *N. alata*.

[†] In *N. langsdorffii* the centromere of the large pair classified as submedian approaches rather closely a median position.

present on both arms. The extremely large proximal satellite of *N. langsdorffii* gives its genom some morphological distinction. This satellite at times appears as large as the shortest chromosome in the complement and approximately one-fourth the length of the chromosome of which it is a part, the thread being almost as long as the satellite itself. The pair exhibiting this satellite is classified as submedian (cf. table 2) although exclusive of the satellite it falls into the subterminal category and was so referred to earlier (Avery, 1938). It has been reported (Avery, *l.c.*) that the two satellited pairs in *N. alata* are indistinguishable, both bearing "small satellites,"

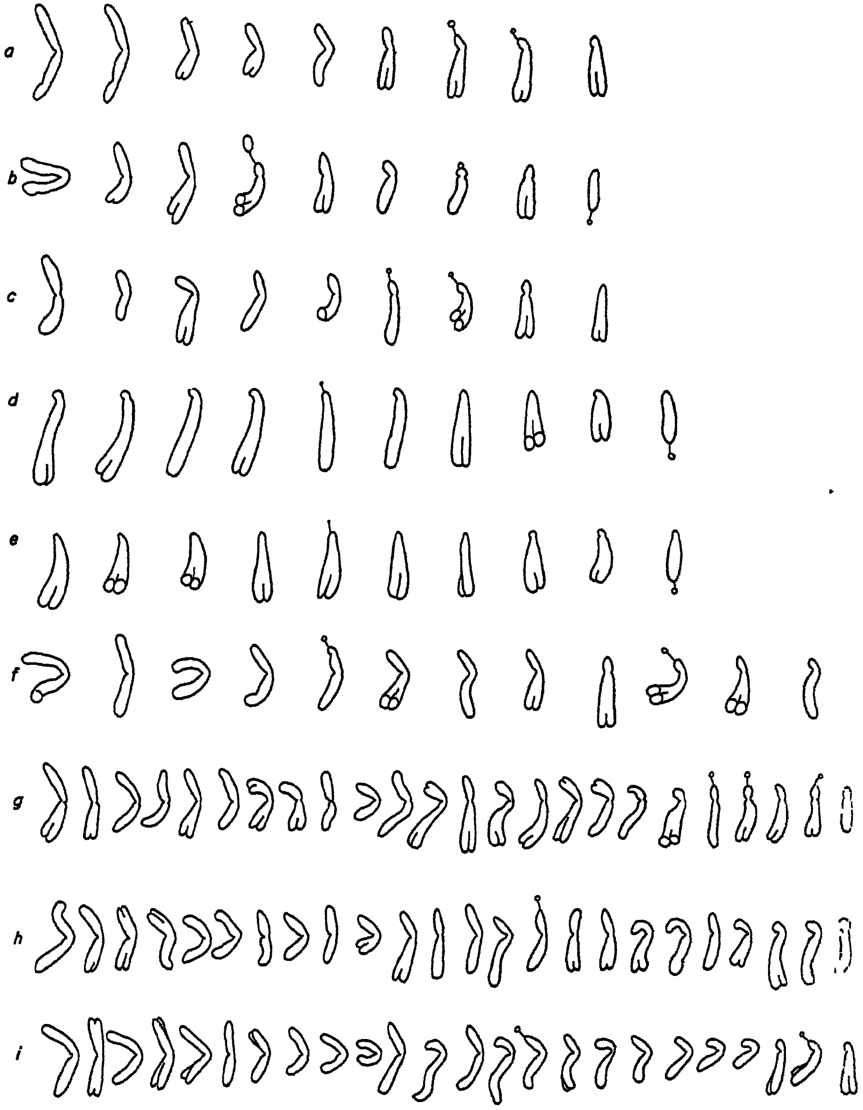

Fig. 5. Karyotypes of section *Alatae*. *a*, *N. alata* ($4\,m + 2\,sm + 3^2\,st$). *b*, *N. langsdorffii* ($2\,m + 4^1\,sm + 3^1\,st$). *c*. *N. bonariensis* ($2\,m + 3\,sm + 4^2\,st$). *d*, *N. longiflora* ($10^2\,st$). *e*, *N. plumbaginifolia* ($10^2\,st$). *f*, *N. sylvestris* ($3\,m + 5^1\,sm + 4^1\,st$). *g*, *N. repanda* ($10\,m + 8\,sm + 6^3\,st$). *h*, *N. stocktonii* ($10\,m + 11^1\,sm + 3^1\,st$). *i*, *N. nesophila* ($10\,m + 11^1\,sm + 3^1\,st$).

but analyses of first pollen grain mitoses confirm the suggestion (Ruttle, 1927) that one satellite is distinctly larger than the other. The smallest subterminal pair in *N. langsdorffii* is also the smallest chromosome in the 9-paired species group. Both in root-tip and first pollen grain mitoses its satellite appears on the periphery of the metaphase plate and is probably distal in relation to the centromere. Its position has been so represented in figure 5 although confirmatory anaphase evidence is at present lacking. As shown in figure 5, *c*, chromosome No. 7 possesses a terminal knob to which Avery (1938) referred as evidence of a third pair of satellites in *N. langsdorffii* which had "partly lost its nucleolus-producing function since this pair shows a satellite-like body which is close to the head of the chromosome but seldom separated from it by a distinct thread." Since in first divisions of the microspore this structure is never provided with a thread, and knowledge of its function is lacking, the pair involved is not classified as satellited.

The two 10-paired species, *N. longiflora* and closely related *N. plumbaginifolia*, possess karyotypes which are practically identical, each consisting of ten subterminal pairs of chromosomes, two pairs with satellites, one proximal and the other distal. Size distinctions between the chromosomes within each genom are not marked except that two pairs in each are somewhat shorter than the rest. Avery (*l.c.*) comments on the smaller size ("shorter and narrower") of the chromosomes of *N. plumbaginifolia* and reports, on the basis of number of nucleoli observed, that *N. plumbaginifolia* possesses one satellited pair and *N. longiflora* two such pairs. It now appears that size distinction between the karyotypes of the two species is slight and that in number and position of satellites the two species are identical. In the latter respect recent analyses confirm the report (Resende, 1937) of two satellites in *N. longiflora*; one extremely small, proximal satellite on one of the longer pairs of chromosomes, and a considerably larger distal satellite on one of the two shortest pairs in the genom. Various other investigators apparently observed only the distal satellites on the short chromosomes, for they comment upon "more or less distinct distal constrictions" (Hollingshead, 1929) and "additions on the distal end which may be satellites" (Sarana, 1934). As just noted, in first pollen grain mitoses of both *N. longiflora* and *N. plumbaginifolia* these satellites appear as rather large chromosomal segments separated from the distal ends of one of the shortest pairs of chromosomes by threads. Anaphase studies of *N. plumbaginifolia* have confirmed the distal position of the satellite. Another characteristic feature of chromosome morphology in the two 10-paired species is the position of the centromere, which in the majority of the pairs is so nearly terminal that the short arms are at times indistinguishable even as "heads." In general, however, the chromosomes of both *N. longiflora* and *N. plumbaginifolia*, as seen in first pollen grain mitoses, exhibit a somewhat "headed" condition which is variable in expression and thus difficult to represent (cf. fig. 5, *d*, *e*).

The karyotype of 12-paired *N. sylvestris* as determined in pollen grain studies is $3\ m + 5^1\ sm + 4^1\ st$. This analysis confirms that reported by Goodspeed and Avery (1939), but differs slightly from the formula ($9\ m$ or $sm + 3^1\ st$) earlier reported by the author (1934); from that of Webber (1930), and of Brooks (1934), both of whom classify one of the submedian pairs as subterminal; and from that of Kostoff (1943), who identifies one of the submedian pairs as median. A subdivision of the chromosomes of this genom into eight types (Sarana, 1934) does not appear justified. On the other hand, such details of chromosome morphology as position of centromere, size and flexure of chromosomes, variation in arm ratio, presence or absence of satellites, and occurrence of additional constrictions, have now made it possible to identify every chromosome in the genom (Goodspeed and Avery, 1939; 1941). For example: (1) of the three median pairs, No. 1 and No. 3 (fig. 5, *f*) consistently appear more sharply flexed than No. 2; (2) near the middle of the longer arms of the longest submedian pair, No. 4, there occur additional constrictions reflected in flexure at that point; (3) the submedian pair, No. 5, is satellited and is further distinguished by an unusual morphological feature, a spherical pycnotic knob at the end of the short arm to which is attached the satellite thread; and (4) three of the four subterminal pairs, one of them the satellited one, vary only slightly in length and in arm ratio, whereas the fourth is distinctly shorter and has a greater arm ratio than has any one of the other three.

It is now known that the three 24-paired species of section *Alatae*, *N. repanda*, *N. stocktonii*, and *N. nesophila*, possess closely similar karyotypes of predominantly median or submedian chromosomes. Thus, the karyotype of *N. repanda* is 10 m + 8 sm + 6^3 st, and that of *N. stocktonii* and *N. nesophila*, 10 m + 11^1 sm + 3^1 st. In at least one submedian pair in each complement an additional constriction is indicated by a flexure in the longer arm. In subterminal chromosomes the centromere position is well marked and occurs an appreciable distance from the end, so that the short arms usually appear as distinct spherical "heads." Within each of the three genoms the range in chromosome length is considerable whereas between them there is little difference, although the chromosomes of *N. nesophila* appear to be somewhat shorter than those of the other two species.

Taxonomically, the five 9- and 10-paired species represent a cluster or nucleus in which various characters that give identity to section *Alatae* are exhibited in common. On the other hand, these species are separable on the basis of somewhat prominent distinctions in external morphology. In terms of chromosome morphology, this species cluster shows marked resemblances and also dissimilarities. Among the three 9-paired species it is possible to homologize chromosomes on the basis of size and other distinguishing features, although differences in position of centromere resulting from quantitative chromosomal alterations are reflected in the karyotype formula of each species. The increase both in submedian and, particularly, in subterminal chromosomes from *N. alata* to *N. bonariensis* reaches its culminaiton in *N. longiflora* and *N. plumbaginifolia* without destroying fundamental genic and structural similarities responsible for the extent of pairing in F_1 hybrids which gives evidence of fundamental relationship within the species cluster (Avery, 1938). The 12-paired species, *N. sylvestris*, although outlying in certain respects, was placed in section *Alatae* because of general morphological resemblances to the other species of this section (Goodspeed, 1945*a*). Similarly, in karyotype pattern it is not unrelated to the 9-paired species. As already noted (p. 354), the genom of *N. sylvestris* can be recognized in that of *N. tabacum*. Close relationship taxonomically unites 24-paired *N. repanda*, *N. stocktonii*, and *N. nesophila*, and their similarity in floral morphology to the 9- and 10-paired species places them in section *Alatae*. They are doubtless derivatives of a common amphidiploid ancestor, and evidence from meiotic chromosome behavior in appropriate F_1 interspecific hybrids and from chromosome morphology suggests that one of its parents may have been a 12-paired species, at present unknown, which was related to the cluster of 9- and 10-paired species (cf. Goodspeed, 1945*b*).

Section *Noctiflorae*.—The three 12-paired species of this section known cytologically are approximately equivalent in karyotype pattern. The fourth, *N. ameghinoi*, is not in cultivation. With the exception of one submedian pair in *N. petunioides*, only subterminal chromosomes occur in the three species. As will be noted, the karyotypes of *N. acaulis* (fig. 6, *a*) and *N. petunioides* (fig. 6, *c*) are represented by haploid genoms selected from diploid metaphase plates of root-tip mitoses, and that of *N. noctiflora* (fig. 6, *b*) from first pollen grain mitoses. Relative size distinctions are therefore not accurately expressed, since chromosomes are somewhat more expanded in metaphase of first pollen grain mitoses than in root-tip mitoses. However, the outstanding size in the section, and indeed in the entire genus, of the *N. acaulis* complement is striking. Characteristic of the species of the *Noctiflorae*, particularly of *N. acaulis*, is the absence—as in many of the chromosomes of *N. longiflora* (cf. p. 358)—of marked constrictions indicating the position of the centromere. *N. acaulis* and *N. petunioides* each possess two subterminal pairs bearing satellites, one of them distal in the former species. In *N. petunioides* the satellite on the smaller pair frequently lies at the periphery of the plate, but it is apparently on the short arm of the chromosome (proximal). Three pairs in *N. noctiflora* possess satellites, two proximal, one of them of considerable size, and one distal. The identity of the *Noctiflorae* on the basis of external morphology and distribution is paralleled by the marked similarity just referred to in the chromosome morphology of the species comprising this section.

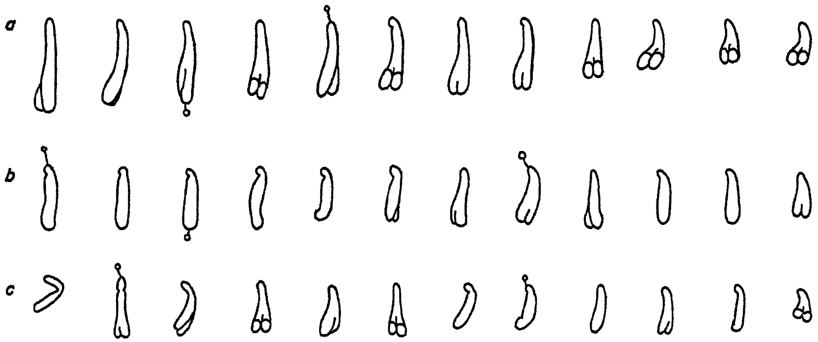

Fig. 6. Karyotypes of section *Noctiflorae*. *a*, *N. acaulis* (12^2 *st*). *b*, *N. noctiflora* (12^3 *st*). *c*, *N. petunioides* ($1\,sm + 11^2\,st$).

Section *Acuminatae*.—As seen in table 2, seven 12-paired species and three 24-paired species comprise section *Acuminatae*. Of the 12-paired species, the karyotype of *N. pauciflora* is not represented in figure 7 because this species is so nearly identical with *N. acuminata*. The remaining six 12-paired species are divided karyologically into two groups: in *N. acuminata*, *N. attenuata*, *N. corymbosa*, and *N. miersii* the karyotype is $2\,m + 6^1\,sm + 4^1\,st$; in *N. spegazzinii* and *N. linearis*, with much smaller chromosomes, it is $1\,m + 3^1\,sm + 8^1\,st$. Recent analyses confirm earlier studies (Goodspeed, 1934) of *N. attenuata* and *N. miersii*, but the formula of *N. acuminata* given above represents a reinterpretation of the karyotype earlier reported as $9\,m$ or $sm + 3^1\,st$. The karyotypes of *N. corymbosa*, *N. spegazzinii*, and *N. linearis*, reported here for the first time, are based upon comparative studies of root-tip and first pollen grain mitoses. The chromosomes of *N. spegazzinii* and of *N. linearis* are uniformly small; indeed, among the smallest in the genus. The genoms of the other 12-paired species are characterized not only by larger chromosomes throughout, but also by sharp intragenomic distinctions in size, particularly apparent in *N. acuminata* and in *N. attenuata*. In one of the longer submedian pairs in the species of this latter group, additional constrictions occur near the ends of the longer arms, and in some of these same species the subterminal chromosomes are characterized by well-marked centromere position and conspicuous "heads." Of the three 24-paired amphidiploid species, *N. bigelovii* and

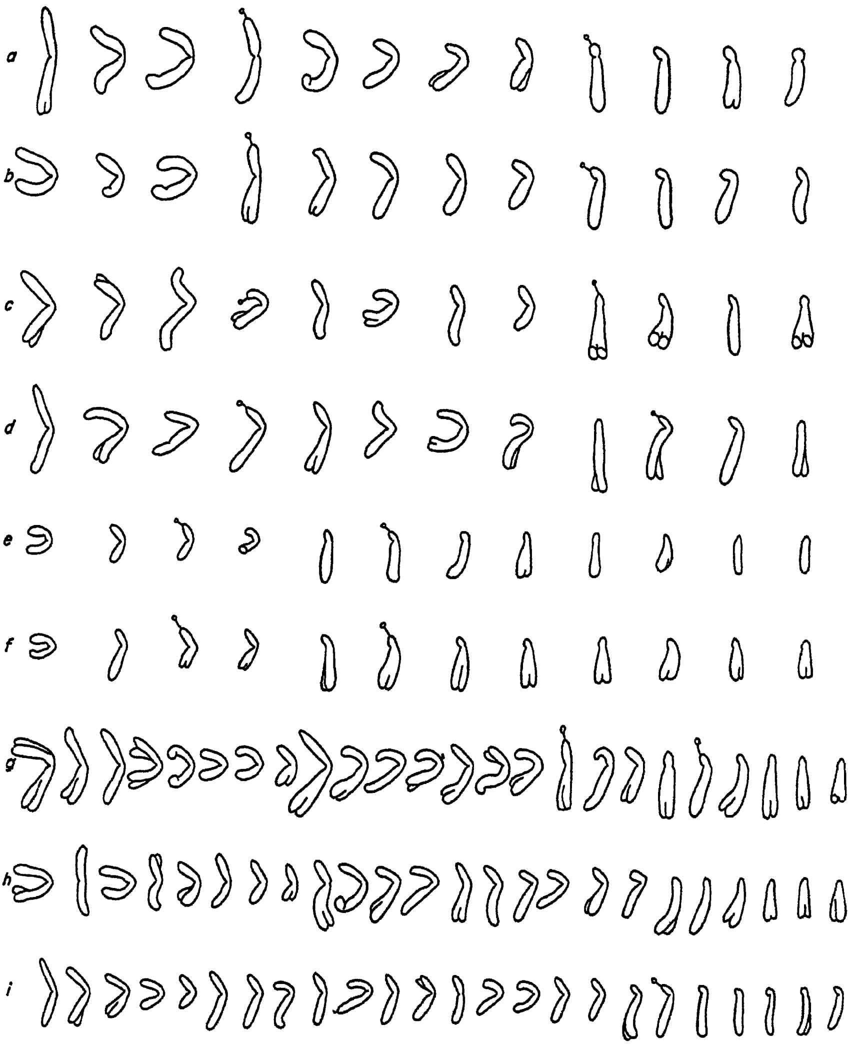

Fig. 7. Karyotypes of section *Acuminatae*. *a*, *N. attenuata* ($2m + 6^1\, sm + 4^1\, st$). *b*, *N. corymbosa* ($2\,m + 6^1\, sm + 4^1\, st$). *c*, *N. acuminata* ($2\,m + 6^1\, sm + 4^1\, st$). *d*, *N. miersii* ($2\,m + 6^1\, sm + 4^1\, st$). *e*, *N. spegazzinii* ($1\,m + 3^1\, sm + 8^1\, st$). *f*, *N. linearis* ($1\,m + 3^1\, sm + 8^1\, st$). *g*, *N. bigelovii* ($8\,m + 10^1\, sm + 6^1\, st$). *h*, *N. clevelandii* ($8\,m + 10^{1,2}\, sm + 6^{1,2}\, st$). *i*, *N. nudicaulis* ($5\,m + 12\, sm + 7^1\, st$).

N. clevelandii are fundamentally identical in karyotype, differing only in the smaller average size of the chromosomes of the latter species. Although doubtless present, satellites have not been observed in this species. Within the genoms of both species there are marked distinctions in size, two median and two submedian chromosomes being among the longest in each complement. In addition, the short arms of the subterminal pairs appear as conspicuous "heads," and in one of the long submedian pairs additional constrictions occur. The third 24-paired species of the *Acuminatae*, *N. nudicaulis*, with a karyotype of $5\ m + 12\ sm + 7^1\ st$, is characterized by exceedingly small chromosomes, probably the smallest in the genus, relatively uniform in size.

Section *Acuminatae* is taxonomically one of the closely knit subdivisions of the genus. Relationships between the 12-paired species based upon external morphology are obvious, and correspondingly the karyotype pattern is closely similar throughout. Of the 24-paired species, *N. bigelovii* and *N. clevelandii* undoubtedly have a common amphidiploid ancestry, as is indicated not only by similarity in fundamental elements of their external morphology and by the equivalence of their karyotypes, but also by complete pairing in F_1 hybrids between them (Goodspeed, 1945*b*). The first two of these types of evidence, together with the extent and character of pairing in appropriate F_1 hybrids, indicate that a progenitor of the 12-paired members of section *Acuminatae* entered into this amphidiploid origin (cf. also Goodspeed, *l.c.*). With respect to *N. nudicaulis*, similar considerations point to an amphidiploid origin, also involving 12-paired members of this section (cf. also section *Trigonophyllae*, p. 356).

Section *Suaveolentes*.—The karyotypes of the thirteen species comprising this section have been described by Wheeler (1945) and will later be illustrated by her. As may be seen in table 1, the chromosome numbers of this Australian–South Pacific section make up a series beginning with 16 pairs and ending with 24 pairs in which only the numbers 17 and 23 are lacking. In addition, 32-paired varieties or races of the 16-paired species are known. There are four 16-paired, two 19-, 20-, and 24-paired, and one 18-, 21-, and 22-paired species. The range in chromosome length within section *Suaveolentes* is considerable (*ca.* 2 μ to 5 μ), the extremes being present within a single complement of certain species. Even in such instances, however, increase in length within the complement is so gradual that groups of conspicuously long and short chromosomes cannot be recognized as they can elsewhere in the genus, for example in section *Tomentosae*.

In the karyotype formulae listed in table 2 it will be seen that every species of section *Suaveolentes* possesses all three morphological types of chromosomes and that a proximal satellite occurs on a subterminal* pair throughout. From species to species the ratios of combined median and submedian to subterminal chromosomes vary, the relative number of subterminal ones increasing progressively with increase in chromosome number. Exceptions are the 24-paired species *N. fragrans*, in which the relative number of subterminal chromosomes is considerably less than the maximum, and 19-paired *N. benthamiana* and 20-paired *N. megalosiphon*, which show a disproportionately large number of subterminal chromosomes. In addition to the one satellited pair above referred to, in at least eleven of the thirteen species

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* In *N. suaveolens*, *N. maritima*, and *N. goodspeedii*, centromere position in this chromosome pair is on the borderline between submedian and subterminal.

there is another satellite characteristic of median or submedian chromosomes, and in *N. fragrans* a second subterminal pair also may be satellited. The occurrence of an extremely large chromosomal segment separated by a distinct thread from the short arm of a submedian pair is conspicuous in certain races of *N. benthamiana* and is reminiscent of the large satellite of *N. langsdorffii* (cf. p. 357). In all species except *N. benthamiana* from one to four median or submedian pairs show a constriction not apparently associated with centromere or satellite.

Taxonomically most closely related species, in general, possess the same or approximately the same chromosome number. This is true of three members of the 16-paired group of species, of the 18-paired and one of the 19-paired species, and of the 21- and 22-paired ones. On the other hand, one 16-paired species appears to have greatest taxonomic affinity with one of the 20-paired species, and another 16-paired species shows relationships with the 18-paired species. In terms of the proportion of median plus submedian chromosomes to subterminal ones in the thirteen karyotypes, the four 16-paired species, on the one hand, and 19-paired *N. benthamiana*, 20-paired *N. megalosiphon*, and 24-paired *N. debneyi*, on the other, are conspicuous in that the ratio of the two morphological types is approximately 3 : 1 and 1 : 3, respectively. Otherwise, the ratio is approximately 1 : 1 for the 18-, 19-, and 20-paired species and 1 : 2 for the 21-, 22-, and 24-paired species. Taxonomically, *N. benthamiana* and, to a lesser degree, *N. debneyi*, *N. fragrans*, and *N. megalosiphon* depart conspicuously from the group of 16-paired species. Otherwise, there appears to be no consistent relationship between likeness or difference in karyotype and similarity or dissimilarity in external morphology in the Australian–South Pacific species. Wheeler (1945) suggests that the 16- and 24-paired species may represent successive allopolyploid levels based upon ancestral 8-paired species and that the 18-paired to 22-paired species may be the products of hybridization between different euploid levels.

It might be noted that in terms of external morphology the species of section *Suaveolentes* are related to the largely South American sections *Alatae*, *Noctiflorae*, and *Acuminatae* (Wheeler, *l.c.*), and that these sections, especially *Noctiflorae* and *Acuminatae*, show relatively high proportions of subterminal chromosomes by contrast with the remaining two sections of the *Petunioides* and with most species in subgenera *Rustica* and *Tabacum*, in which the number of subterminal chromosomes is low, or only median and submedian chromosomes occur. Assumption of a basic chromosome number of 8 pairs for section *Suaveolentes* further relates this section to section *Alatae*, the only American section in which chromosome numbers other than 12 and 24 are today represented.

COMMENT

Of the fifty-eight species of *Nicotiana*, 75 per cent are American in distribution; of these, 85 per cent are South American. The remaining 25 per cent of the genus is Australian or South Pacific. Morphologically, *Nicotiana*, although rather highly polymorphic, is readily distinguishable from other Solanaceous genera, with the possible exception of *Petunia* and, to an appreciably less degree, *Cestrum* and *Salpiglossis*. Apart from subgenus *Petunioides*, which is largely herbaceous, the majority of species are woody and (at least limited) perennials. In the absence of a modern taxonomic organization, and in favor of the recognition of numerous new or little known species, a preliminary revision of the genus, including details concerning distribution and morphology, has recently been made.

Chromosome number is known for fifty-five species. Of the American species, approximately 66 per cent possess 12 pairs, the remaining species being 9-, 10-, or 24-paired. By contrast, none of the Australian–South Pacific species shows 12 pairs and the mode is at 16 pairs, the remaining chromosome numbers forming an almost uninterrupted series between 16 and 24 pairs. On the assumption that the basic chromosome number for *Nicotiana* is 6, 12- and 24-paired species represent polyploid derivatives. From this point of view, the relatively few 9- and 10-paired American species are products of hybridization between 6-paired species which are at present unknown. Eight-paired species, again unknown today, may have had a similar origin and have become responsible through polyploidy for the 16- and 24-paired Australian–South Pacific species. Through hybridization imposed upon such polyploidy, the aneuploid series in that species group could have been derived. In this connection, attention is directed to the morphological similarities between the group in question and the American sections *Alatae*, *Noctiflorae*, and *Acuminatae*. There is here a suggestion that, following a South American origin, the progenitors of section *Suaveolentes* became established in Australia and the South Pacific via Antarctica. The occurrence of 7- and 9-paired species of *Petunia* and morphological resemblances between that genus and *Nicotiana* suggest related 6-paired ancestors for modern representatives of both genera. That polyploidy has actually played a considerable part in the evolution of the genus *Nicotiana* is indicated by such authenticated instances of amphidiploid origin as that of *N. tabacum*, *N. rustica*, and *N. arentsii*.

Karyotypes of fifty-five of the fifty-eight species of *Nicotiana* have been determined. For the genus as a whole no common karyotype pattern obtains. The chromosomes are relatively small to medium, and in terms of centromere position median and submedian chromosomes predominate over subterminal ones in the ratio of 5 to 3. The chromosome morphology of the various taxonomic divisions is in general sufficiently definitive to have significance for interpretation of species origins and relationships. That structural chromosomal reorganizations and alterations in genic constitution have proceeded independently in the evolution of the genus is indicated by the fact that the products of these two processes as reflected, the one in distinctions in karyotypes, and the other in distinctions in external morphology, are often not proportionate. For example, the evolution of the divergent karyotypes of the 9- and 10-paired members of section *Alatae* has apparently occurred without equivalent alterations in the genic constitution of their genoms, as is indicated by close morphological similarities between them, whereas on the other hand the karyotypes of *N. undulata* (subgenus *Petunioides*) and of members of section *Paniculatae* (subgenus *Rustica*) have much in common. However, evidence from chromosome morphology largely substantiates the validity of the relationships expressed by the taxonomic organization adopted. Thus, the three subgenera are characterized by a distinction in the ratio of median and submedian to subterminal chromosomes: *Rustica*, 9 : 1; *Tabacum*, 5 : 2; *Petunioides*, 3 : 2. Corresponding to the relatively close morphological resemblances within subgenus *Rustica*, the karyotype formulae are practically identical for all but one species. Taxonomically, the two other subgenera are progressively somewhat more diversified and, correspondingly, their sections tend to be more or less set apart in terms of chromosome morphology. On the other hand, within the majority of them occur clusters or nuclei of species, and in each section the cluster is characterized by a practically identical karyotype. For example, three of the five species of section *Tomentosae*, subgenus *Tabacum*, most closely related morphologically possess almost equivalent karyotypes, and four of the six sections of subgenus *Petunioides* show a karyotype pattern common to the nucleus species in each case. Finally, the karyotype of each of the nine amphidiploid species reflects in more or less detail the karyotypes of the modern descendants of their putative progenitors. It is to be noted, further, that a large body of evidence dealing with extent of pairing at MI in F_1 interspecific hybrids of *Nicotiana* gives further indication of the validity of the relationships expressed in the taxonomic organization.

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KARYOTYPE EVOLUTION: A CYTOGENETIC STUDY OF SEVEN SPECIES AND SIX INTERSPECIFIC HYBRIDS OF CREPIS

BY

MARTA SHERMAN

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CONTENTS

PAGE

Introduction 369

Materials and methods 371

  Acknowledgments 372

Morphology of species and hybrids 372

Somatic chromosomes of parent species and interspecific hybrids 372

  Nomenclature 372

  Chromosome morphology of parent species 373

  Modification of chromosome length in interspecific hybrids 373

  Behavior of satellites in interspecific hybrids 373

Meiosis in parent species 375

  Pachytene 375

  Diakinesis and metaphase 376

  Anaphase and telophase 377

Meiosis in interspecific hybrids 377

  Pachytene 377

  Diakinesis 377

    Identification of parental chromosomes in diakinesis of F_1 hybrids 378

    Description and interpretation of chromosome configurations observed in diakinesis of interspecific hybrids 379

    Origin of translocations producing these chromosome associations 383

    Apparent absence of reciprocal associations 385

    Frequencies of different types of chromosome associations 386

    Terminalization of chiasmata in the six hybrids 387

  Metaphase, anaphase, and telophase 388

Conclusion and summary 389

Literature cited 394

Plates 395

KARYOTYPE EVOLUTION: A CYTOGENETIC STUDY OF SEVEN SPECIES AND SIX INTERSPECIFIC HYBRIDS OF CREPIS

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INTRODUCTION

INVESTIGATION of various plant genera has shown that the increase or decrease of chromosome numbers characterizing the species within a genus has been a very widespread evolutionary process. Two types of changes in chromosome number have occurred: polyploid changes, in which the unit of change is the entire set, and aneuploid changes, in which the unit of change is one chromosome pair. In the genus *Crepis* the aneuploid changes have been of primary importance. Although the majority of *Crepis* species have a basic number of four, morphological and geographical evidence leads to the conclusion that the primitive basic number is six (Babcock and Jenkins, 1943). The basic haploid numbers range from three to six. Since all of the 6-paired species are primitive and the species most advanced morphologically have four or three pairs, it is inferred that a progressive decrease in basic chromosome number has occurred in *Crepis*. This decrease in basic chromosome number, which has resulted in an aneuploid series, may be said to be the outstanding feature of karyotype evolution in *Crepis*.

One of the first attempts to explain aneuploid changes in chromosome number was advanced by Navashin (1932). Briefly, his "dislocation hypothesis" postulates increase in chromosome number as a result of addition of an extra chromosome, followed by translocations which replace its material with material from other chromosomes of the set, and finally, origin of an individual homozygous for the new chromosome; decrease in chromosome number results from translocations of material from one chromosome to others of the set followed by loss of the unattached centromere, and finally, by origin of an individual homozygous for the new karyotype.

Since Navashin's hypothesis was formulated, it has become increasingly evident that terminal simple translocations occur rarely if at all (Dobzhansky, 1941, p. 105). It was shown by Lewitsky and Sizova (1935) that in *Crepis* all or most of the translocations are reciprocal, although the parts translocated may be extremely unequal. In 1936 Navashin and Gerassimova, having come to the conclusion that all or most of the translocations in *Crepis* are reciprocal, added this feature to the dislocation hypothesis.

It is also possible that hybridization of strains with complementary translocations may produce a hybrid in which all the genetic segments of one chromosome are present in one or more other chromosomes of the set. In this way translocation followed by hybridization and elimination of the extra centromeres and of duplicated material may produce a new karyotype which has one fewer pair of chromosomes but which contains the same structural elements which were present in the original karyotype.

The general principles now recognized as involved in the phylogenetic reduction in chromosome number are: (1) the occurrence of unequal reciprocal translocations which transfer the genetic material of one chromosome to one or more other chromosomes of the set, and (2) loss of the centromere bearing no genetically valuable material. If hybridization is involved in the reduction of chromosome number, the following steps must occur: (1) two independent series of translocations in two separate strains of a species, each of which transfers a different part of the genetic material of one chromosome to one or more other chromosomes of the respective sets, followed by (2) hybridization of the two complementary types, and (3) elimination of the extra centromeres and attached duplicated material.

The basic postulate of both hypotheses, that is, a series of translocations transferring the genetic material of one chromosome to one or more other chromosomes of the set has, until very recently, not been shown to have occurred in nature. In order to provide such a demonstration the following conditions are necessary: (1) a series of closely related species must be found in which decrease in chromosome number has taken place; (2) the species must be crossable so that interspecific hybrids may be obtained; (3) the chromosomes must be small in number and distinguishable by morphology and size throughout the meiotic cycle.

In *Crepis* there are several groups of closely related species in which morphological evidence clearly indicates the phylogenetic relationships, and in which decrease in chromosome number has occurred. The chromosomes are large and sufficiently distinct so that each can be traced through the meiotic stages following pachytene. These species may be crossed and viable hybrids obtained. Investigations of meiosis in the F_1 hybrid between related species with different chromosome numbers make it possible to trace and identify translocations expected on the basis of either of the above two hypotheses, and thus to provide cytological evidence on the processes involved in the decrease in chromosome number.

For these reasons two studies were begun dealing with the process of decrease in chromosome number. Tobgy (1943) studied two species, *Crepis neglecta* ($n = 4$) and *C. fuliginosa* ($n = 3$) and their hybrid; he concluded that the reduced chromosome number in *C. fuliginosa* has been achieved by a single reciprocal translocation, as a result of which the B and C chromosomes of *C. neglecta* gave rise to the B chromosome of *C. fuliginosa.* Other reciprocal translocations involved the A and D chromosomes but these were not responsible for the reduction in chromosome number.

This study of six 5-paired species and one 4-paired species of *Crepis* and their hybrids was undertaken with the aim of tracing, as far as possible, the processes involved in decrease of chromosome number in this group. This investigation has led to the conclusion that reduction in chromosome number in this instance results from transfer of the material of one chromosome to other chromosomes of the set, followed by loss of the unattached centromere, or followed by hybridization of two strains with complementary translocations and subsequent loss of the extra centromeres and duplicated material.

MATERIALS AND METHODS

The seven species studied were *Crepis Kotschyana* Boiss. ($n = 4$), and *C. Thomsonii* Babc., *C. eritreënsis* Babc., *C. foetida commutata* (Spr.) Babc., *C. rubra* L., *C. syriaca* (Bornm.) Babc., and *C. alpina* L. (all with $n = 5$).[1] All seven species belong to the section Hostia (Babcock and Jenkins, 1943). The 5-paired species are grouped together on the basis of external morphology and chromosome number and morphology; the 4-paired species was included in the group by these authors on the basis of evidence of morphological similarity and geographical distribution. Comparisons of the genetic homologies of the chromosomes of these species support the inclusion of *C. Kotschyana* in this group of 5-paired species.

It is certain that the 4-paired chromosome set of *C. Kotschyana* represents a decrease in chromosome number rather than the basic number from which the 5-paired species arose because of the taxonomic position of *C. Kotschyana* in relation to the 5-paired species as determined by Babcock (1946).

Root tips were fixed in Randolph's (1935) "Craf" solution, dehydrated through the n-butyl alcohol series, embedded in paraffine, sectioned at 10μ and stained according to Stockwell's (1934) schedule.

The following technique was used in measuring the mitotic chromosomes. Only those chromosomes were measured which were lying so nearly in one plane that no focusing was necessary to follow the chromosome through its entire length. A camera lucida line drawing was made of each chromosome, the line being drawn through the center of the chromosome and extending from one end of the chromosome to the other. The line drawings were carefully measured with 1 mm. calipers and the measurements obtained were converted to micra.

Buds were fixed in acetic alcohol (3 parts absolute alcohol: 1 part glacial acetic acid) for twenty-four hours; the buds were then washed and stored in 70 per cent alcohol.

Meiotic figures were studied entirely from pollen mother cells in acetocarmine smears. It was found necessary to pretreat the material in a 4 per cent solution of iron alum for fifteen minutes to one hour before smearing in acetocarmine.

Slides were made permanent by the following procedure: the cover slip was floated off in a solution of 1 absolute alcohol: 1 glacial acetic acid; the slide and cover slip were immersed for one minute in a solution of 3 absolute alcohol: 1 glacial acetic acid, and for a minute each in two changes of absolute alcohol; the slide was sealed with a drop of euparal. Permanent slides have remained in excellent condition over a period of more than a year.

Drawings were made with the aid of a camera lucida at a magnification of

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[1] The strains used had the following accession numbers: *C. Kotschyana*, 2340; *C. Thomsonii*, 3208; *C. eritreënsis*, 3005A; *C. foetida commutata*, 3426 and 3394; *C. rubra*, 3452; *C. syriaca*, 3231; *C. alpina*, 3441.

3500, using a Leitz 2.0 mm. N.A. 1.32 apochromatic objective and Zeiss 20 × compensating oculars. Drawings of somatic chromosomes in plates 16 and 17 were reduced to 2430 × in reproduction, and the drawings of meiotic chromosomes in plates 18–21 were reduced to a magnification of 1050.

Photomicrographs were made at a magnification of 1300 with a Bausch and Lomb 2.0 mm. N.A. 1.30 apochromatic objective and a 15 × compensating ocular, and were reduced to 1050 × in reproduction. A Leitz Makam camera was used.

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MORPHOLOGY OF SPECIES AND HYBRIDS

A thorough morphological study of the seven species was made and the F_1 hybrids were carefully compared in all details. These studies are not reported here. The species are described and illustrated in Professor Babcock's monograph on the genus *Crepis* (1946). In the hybrids the majority of quantitative characters were intermediate between the two parents; several qualitative characters were completely dominant and others exhibited variation in type of inheritance in the different hybrids. It appeared that almost all of the quantitative and qualitative plant characters measured in this investigation, which are to a large extent those differentiating the species in this group, are controlled by several or many pairs of factors, as well as by accessory factors which probably exert a modifying or inhibiting effect.

SOMATIC CHROMOSOMES OF PARENT SPECIES AND INTERSPECIFIC HYBRIDS

NOMENCLATURE

The karyotypes of the seven species show considerable similarity (pl. 16). Comparison of the morphology and structure of *Crepis* chromosomes is facilitated by the use of the terminology initiated by Navashin (1925). Accordingly, the A chromosome is a large chromosome with a long short arm; the B is a large chromosome with a shorter short arm; the C is a comparatively small chromosome with a short short arm; the D is the satellite-bearing chromosome, and the E is a small, approximately equal-armed chromosome.

Although the *C. Kotschyana* complement lacks the E chromosome, its A, B, C, and D chromosomes are very much like the corresponding chromosomes of the 5-paired species.

The similarity implied by this system of nomenclature, as proposed by Navashin, refers only to the gross morphology of the chromosomes and not to their genetic or structural homology. However, evidence presented in a later section shows that in the group of species here studied, chromosomes of similar morphology (and thus given the same letter designations) are also largely similar structurally. That is, from their meiotic behavior in hybrids it may be inferred that they are essentially homologous chromosomes.

CHROMOSOME MORPHOLOGY OF PARENT SPECIES

The measurements of the metaphase chromosomes of the parent species were taken from root tips of those species, since changes in chromosome length were observed in the hybrids. In each case the root tips were collected from several plants in the population.

The chromosomes of any one complement are similar in width, and no measurable difference was observed in the width of the chromosomes of the seven species (pl. 16).

The data on chromosome lengths of the species are arranged in table 1, and the data on proportions of arm lengths are presented in table 2.

The individual chromosomes of the 5-paired species cannot be compared in length with the corresponding four chromosomes of *C. Kotschyana* because even without the cytological evidence to be presented later, it could be postulated that, in derivation of *C. Kotschyana* from a 5-paired ancestor, the majority of the chromatin material of the E chromosome had been transferred to the other chromosomes of the set rather than lost, since it has been shown many times (*Drosophila, Triticum*) that loss of one pair of chromosomes has a lethal effect. It may be significant that the individual chromosomes of *C. Kotschyana* are longer than the corresponding chromosomes of the 5-paired species (table 1).

The correlation between the relationship of the 5-paired species to *C. Kotschyana* based on external morphology and that based on somatic chromosome morphology supports the consideration of somatic chromosome morphology as a morphological character, subject to change as are other morphological characters, and one which, in conjunction with other such characters, provides additional evidence about taxonomic relationship.

MODIFICATION OF CHROMOSOME LENGTH IN INTERSPECIFIC HYBRIDS

It has been observed (Sherman, unpublished) that in certain interspecific hybrids the chromosome sets undergo a change in length, the deviation ranging from $-3.05\mu \pm 0.36$ to $+3.33\mu \pm 0.30$. Variation in length of a chromosome set in an interspecific hybrid has previously been observed in *Crepis* by Navashin (1934).

BEHAVIOR OF SATELLITES IN INTERSPECIFIC HYBRIDS

"Differential amphiplasty," described by Navashin (1928, 1934) as disappearance of the satellite from the D chromosome, occurs in some of these interspecific hybrids (pl. 17). In *Thomsonii* × *Kotschyana* neither D chromosome satellite is present. In *foetida commutata* × *Kotschyana* the *Kotschyana* D chromosome satellite remains and that of the 5-paired species fails to appear; in *Kotschyana* × *syriaca* the *syriaca* D chromosome satellite remains whereas that of the

TABLE 1

CHROMOSOME LENGTHS OF THE SEVEN *Crepis* SPECIES, IN MICRA

(Twenty chromosomes of each type were measured)

Chromosome type	A	B	C	D	E	Total
Kotschyana............................	7.87±.10	7.41±.09	4.91±.08	5.32±.08	....	25.53±.09
Thomsonii............................	6.54±.08	6.13±.07	3.96±.06	4.43±.05	4.50±.07	25.56±.15
Eritreënsis............................	6.51±.09	6.20±.08	4.00±.07	4.34±.06	4.61±.07	25.67±.16
Foetida commutata.....................	6.27±.09	5.97±.08	3.87±.07	3.86±.06	4.54±.07	24.52±.17
Rubra..............................	7.40±.13	7.27±.08	3.93±.07	4.63±.13	4.21±.07	27.45±.22
Syriaca............................	6.09±.06	6.40±.07	3.23±.06	3.13±.10	3.67±.06	22.52±.16
Alpina............................	6.31±.11	6.44±.07	3.31±.05	3.05±.06	3.39±.05	22.51±.17

Kotschyana D chromosome does not appear. Those hybrids in which the phenomenon is not observed and in which both satellites are present are *Kotschyana* × *alpina*, *eritreënsis* × *Kotschyana*, and *Kotschyana* × *rubra*.

Navashin found that the change, if any, occurs in a certain interspecific hybrid regardless of the direction of the cross; therefore it is not a cytoplasmic effect. Reciprocal hybrids were not obtained in this experiment, but it seems probable that this aspect of satellite behavior would be the same in these *Crepis* species as it was in those studied by Navashin.

At any rate, it is probable that the nonappearance of the D chromosome satellite is genetically controlled. Such genetic control is believed to be accomplished by a separate mechanism from that responsible for the variation in chromosome length in certain of these interspecific hybrids, for it has been found (Sherman, unpublished), that there is no connection between the presence or absence of satellites in interspecific hybrids and the variation in chromosome length.

TABLE 2

THE RATIOS OF CHROMOSOME ARM LENGTHS OF THE SEVEN *Crepis* SPECIES—SHORT/LONG ARM

(Twenty chromosomes of each type were measured)

Chromosome type	A	B	C	D	E
Kotschyana	0.58	0.37	0.06	0.20	....
Thomsonii	0.44	0.39	0.70	0.23	0.89
Eritreënsis	0.47	0.41	0.73	0.23	0.86
Foetida commutata	0.49	0.43	0.83	0.28	0.93
Rubra	0.40	0.37	0.64	0.09	0.84
Syriaca	0.37	0.22	0.32	0.27	0.88
Alpina	0.36	0.21	0.31	0.27	0.80

MEIOSIS IN PARENT SPECIES

A general description of meiosis as observed in the seven species investigated will not be given, since these observations agree with the detailed description by Richardson (1935) of meiosis in *C. capillaris* and *C. tectorum*. The chromosomes will be described during certain stages of meiosis in which their behavior is of particular interest and importance.

PACHYTENE

In this material the pachytene chromosomes were so entangled that even in the most favorable preparations it was not possible to identify any of the chromosomes or to trace any chromosome for more than about one-third of its length. However, it was possible to observe the extent of pairing of the chromosomes as a whole and to observe in detail paired chromosome segments which were free.

When pachytene cells of the different species were observed, it was found that in general the homologous bivalents are closely paired and that the paired chromomeres are similar in size and shape. A detailed examination was made of two species, *C. Kotschyana* and *C. Thomsonii,* by following all the paired pachytene threads which were free and which could be compared chromomere by chromomere. It was found that there are a few exceptions to the general rule of complete and homologous pairing; however, all of these exceptional segments were very small, including only one to four chromomeres, and are not considered to be significant deviations from normal association of chromosomes.

DIAKINESIS AND METAPHASE

In diakinesis the chromosomes form every type of bivalent possible, with chiasma frequencies ranging from 1 to 4 per bivalent. Chiasmata are not localized but appear in terminal as well as interstitial positions, suggesting that chiasma formation in these *Crepis* species is initiated at random. Generally, the amount of terminalization is not high in *Crepis,* and in this group, although significantly more terminalization is evident in metaphase than in diakinesis, it is far from complete. The number and distribution of chiasmata in diakinesis of the seven species studied are presented in table 3.

TABLE 3

FREQUENCY AND DISTRIBUTION OF DIAKINESIS CHIASMATA IN THE SPECIES AND INTERSPECIFIC HYBRIDS

Species	Number of chiasmata per cell		Terminalization coefficient	
	Parent	Hybrid	Parent	Hybrid
Kotschyana	7.1±.19	....	0.30	....
Thomsonii	8.0±.19	5.2±.15	0.27	0.46
Eritreënsis	8.7±.16	5.6±.21	0.38	0.46
Foetida commutata	6.3±.12	6.4±.12	0.42	0.48
Rubra	8.9±.24	6.9±.11	0.38	0.42
Syriaca	6.8±.11	5.7±.16	0.25	0.46
Alpina	6.6±.14	5.9±.14	0.28	0.44

It may be observed in plate 16 that the short arm of the *C. Kotschyana* C chromosome is minute. Nevertheless, interpretations of certain meiotic configurations in the interspecific hybrids depend upon the formation of a chiasma in this arm. Therefore it is of interest to determine its frequency in the pure species. Unfortunately it is not possible to distinguish between the C and D chromosomes of this species at metaphase. However, it was observed that in two of the 50 *C. Kotschyana* metaphase cells studied a chiasma was present in both arms of each of the small chromosome pairs, that is, in both the C and D chromosomes. Therefore a chiasma is found in the minute short arms of the C chromosomes in a minimum of 4 per cent of the *C. Kotschyana* metaphase cells. In 32 per cent of the *C. Kotschyana* metaphase cells a chiasma was observed in the short arms of one of the small chromosome pairs, either the C or D chromosomes; thus the actual frequency of chiasma formation in the short arms of the *C. Kotschyana* C chromosomes is probably higher than 4 per cent.

ANAPHASE AND TELOPHASE

The remaining stages of the meiotic divisions were normal except in *C. rubra*, in which lagging chromosomes and bridges were observed. Since a relatively high number of chiasmata were formed regularly at diakinesis and since metaphase was normal, this strain was crossed with *C. Kotschyana* to produce the *Kotschyana* × *rubra* hybrid needed for this investigation.

MEIOSIS IN INTERSPECIFIC HYBRIDS

PACHYTENE

The somatic chromosome complements of the 5-paired species range from 108 per cent (*C. rubra*) to 88 per cent (*C. alpina*) as long as the *C. Kotschyana* complement. If the same length relations exist in meiosis, the expectation would be that in the hybrids a considerable portion of the chromosomes of one species would be either unpaired or autosyndetically paired.

Pachytene cells of two hybrids, *Kotschyana* × *rubra* and *foetida commutata* × *Kotschyana*, are shown in plate 18, figures 1 and 2; these cells are typical of pachytene cells of all the hybrids. It will be observed that in each case all the chromosome ends are paired, and furthermore, that there is a remarkable degree of pairing along the entire length of the chromosomes of the two species. Although occasionally small unpaired regions are seen, these are never extensive enough to account for differences in length of the two complements. Unequal somatic chromosome length and equal pairing in pachytene in *Crepis* has also been reported by Tobgy (1943).

Since the chromosomes of the above species enter the meiotic cycle unequal in length, it may be suggested that the forces which bring about chromosome pairing in meiosis may be responsible for producing pachytene chromosomes of nearly equal length.

DIAKINESIS

If most of the genetically active material of the E′ chromosome[2] has been translocated to one or several of the other chromosomes of the set, there should be some evidence of these translocations in meiosis of hybrids between *C. Kotschyana* and the 5-paired species. Since these translocations will be present in the heterozygous condition in the hybrids, and since the chromosome pairs, and in many cases the individual chromosomes, can be identified, it should be possible to determine, in part at least, to which chromosome or chromosomes of the *C. Kotschyana* set portions of the E′ chromosome were translocated. Similarly, any other translocations which may have occurred in *C. Kotschyana* or in one of the 5-paired species will be present in the heterozygous condition and may be identified.

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[2] The E chromosome of the 5-paired ancestor of *C. Kotschyana* is designated the E′ chromosome.

IDENTIFICATION OF PARENTAL CHROMOSOMES IN DIAKINESIS OF F_1 HYBRIDS

It was found that an outstanding change in chromosome length takes place in meiosis of these interspecific hybrids: in diakinesis of each hybrid the length of the A^X[3] has decreased approximately half. The width of this shortened chromosome remains unchanged.

It should be pointed out that this decrease in length of the A^X in meiosis is not related to the variation in length of chromosome sets and of individual chromosomes which has been observed in mitosis of certain interspecific hybrids (see above, p. 373).

In a typical *C. Kotschyana* diakinesis cell (pl. 18, fig. 3), there are four large chromosomes, the AA and BB pairs, and four small chromosomes, the CC and DD pairs. In typical diakinesis cells of the 5-paired species (pl. 18, figs. 4, 5), there are the four large A and B chromosomes, and six small chromosomes, the CC, DD, and EE pairs. Diakinesis cells of the F_1 hybrids, however, exhibit three large chromosomes and six small ones instead of the complement of four large chromosomes and five small ones expected on the basis of the chromosome sets of the parents (pl. 18, figs. 6, 7). These configurations are typical of all six hybrids.

According to the relative sizes of the parent chromosomes, the large nearly equal chromosome pair (pl. 18, fig. 6) is either the AA or BB pair, and the large chromosome of the very unequal pair is either an A or a B chromosome.

In the trivalent shown in plate 19, figure 2, the unequal pair of chromosomes is associated with the E chromosome (this is a frequent trivalent configuration and is found in all six hybrids). Observe that there is one small chromosome attached to each end of the large chromosome; the two small chromosomes are never adjacent in this type of configuration. The large chromosome of the trivalent is paired with the E^X. Since there is no evidence for the regular occurrence of autosyndesis in these hybrids the large chromosome must therefore be either the *C. Kotschyana* A or B chromosome.

It may be observed in metaphase configurations (pl. 21, figs. 2, 4) that the short arm of the large chromosome of the unequal pair is longer than that of either chromosome of the large nearly equal pair. In *C. Kotschyana* the short arm of the A chromosome is longer than the short arm of the B chromosome (pl. 16; table 2); therefore the large chromosome of the very unequal pair of chromosomes is the A^K.[4]

All possible interpretations of the small chromosome paired with the large A^K were considered and it was found that if the small chromosome is assumed to be the A^X autosyndetic pairing is rarely observed, whereas the frequent occurrence of autosyndetic pairing must be postulated on the basis of any other interpretation. Therefore it is concluded that the small chromosome of the unequal pair is the A^X.

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[3] A^X refers to the A chromosome of any 5-paired species.

[4] The linear capital letter indicates the chromosome and the superior letter the species which the chromosome represents.

In occasional cells there are two large nearly equal pairs of chromosomes (see pl. 18, fig. 8). In this case the two large pairs are probably A^KA^X and B^KB^X, whereas the two D chromosomes are associated with the nucleolus and the three small chromosomes forming the trivalent are C^KC^X and E^X. Such cells are rare; it is possible that occasionally the reaction or reactions responsible for the decreased size of the A^X may fail to take place or to reach the necessary threshold. The cell shown in plate 18, figure 8 should be compared with that in plate 18, figure 7 from the same slide, in which the A^X is seen to be reduced in size.

It seems most probable that the large chromosome of the unequal pair is the A^K and its small partner is the A^X, which has decreased approximately half in length without changing in width; the large nearly equal pair of chromosomes associated with the nucleolus is the DD pair. The remaining small pair of chromosomes is the CC pair, and the small univalent is the E chromosome (pl. 18, fig. 6.)

DESCRIPTION AND INTERPRETATION OF CHROMOSOME CONFIGURATIONS OBSERVED IN DIAKINESIS OF INTERSPECIFIC HYBRIDS

Multivalent configurations.—Space does not permit a description of the multivalent configurations found in diakinesis of all six interspecific hybrids. However, the majority of the different types of diakinesis configurations which were found are described below. The data obtained from study of the diakinesis configurations of the six hybrids are arranged in table 4.

CC=E.[5] It may be observed in table 4 that the configuration which appears most frequently in diakinesis of each interspecific hybrid is the CC=E trivalent. It is assumed that the association of the E^X with the C^K occurs because of the existence of homologous regions in these two chromosomes, and therefore that one of the translocations preceding the "loss" of the E′ chromosome involved transfer of a portion of the E′ from the 5-paired ancestor to the C chromosome of *C. Kotschyana.* From the frequency with which CC=E configurations are observed, it may be inferred that the translocated segment was relatively large. Table 2 and plate 16 show that the short arm of the *C. Kotschyana* C chromosome is minute. Therefore the conclusion is reached that a large segment of the E′ chromosome was translocated to the *long* arm of the *C. Kotschyana* C chromosome.

The CC=E configurations were of several different types (pl. 19, figs. 1, 3, 4), the configuration depending upon the arrangement of the paired segments at pachytene and upon the number and arrangement of the chiasmata. In order to form such diverse diakinesis trivalents as those referred to above, pairing must have occurred between various regions of the C^{KL} and E^{X} in pachytene; for example, the trivalents shown in plate 19, figure 1, *a* and *i*, depend upon a chiasma formed between the subterminal to terminal regions of both the C^{KL} and the E^{X}, whereas the trivalents shown in plate 19, figure 1, *b* and *h*, depend upon a chiasma formed between the subterminal to terminal regions of the E^{X} and the median (or closer to the centromere) region of the C^{KL}. Such differences in pachytene arrangement of the C^{KL} and E^{X} indicate that there has been rearrangement of the E′ material in the C^{KL} following the initial translocation.

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[5] The configurations are abbreviated as follows: The linear capital letter refers to the chromosome, the first superior letter refers to the species which the chromosome represents, and the second superior letter refers to the arm of the chromosome. A comma is used between two arms of the same chromosome; a hyphen indicates one or more chiasmata between two homologous chromosomes; an equal sign represents one or more chiasmata between two non-homologous chromosomes. Thus $A^X\text{-}A^K=C^{XL}$, $C^{XS}\text{-}C^{KS}$, $C^{KL}=E^X$ may be translated: the A chromosome of the 5-paired species is paired with the *C. Kotschyana* A chromosome, which is paired with the long arm of the C chromosome of the 5-paired species; the short arm of this C chromosome is paired with the short arm of the *C. Kotschyana* C chromosome; the long arm of the *Kotschyana* C chromosome is paired with one arm of the E chromosome of the 5-paired species.

TABLE 4

PERCENTAGES OF VARIOUS CONFIGURATIONS AT DIAKINESIS IN THE SIX HYBRIDS

Configurations	*Fc* × *Ko*	*Th* × *Ko*	*Er* × *Ko*	*Ko* × *Ru*	*Ko* × *Sy*	*Ko* × *Al*
$4_{II}+1_{I}$	22	31	39	17	39	40
CC=E	48	16	36	55	23	40
AA=E	4	9	3	10	11	7
AA=D	1	1	3	—	—	—*
BB=E	1	—	—	—	—	—
CC=D	1	—	—	—	—	—
DD=E	—	3	3	2	—	1
BB=D	—	1	—	1	2	—
DD=A	—	—	—	—	—	1
DD=B	—	—	—	—	1	—
BB=DD	8	2	6	5	1	1
AA=CC	5	3	—	1	—	—
DD=AA	2	—	—	—	2	—
BB=CC	1	1	—	—	—	—
BB=AA	—	1	3	—	—	—
CC=D=E	—	1	—	—	—	—
AA=CC=E	10	3	3	10	3	1
AA=BB=E	1	—	—	—	—	1
AA=DD=E	1	—	—	—	3	—
DD=BB=E	—	1	—	—	—	—
CC=DD=E	—	—	—	—	1	—
BB=DD=AA	1	—	—	2	—	—
AA=CC=DD	1	—	—	—	—	—
AA=BB=CC	—	—	—	1	—	—
BB=AA=CC=E	1	—	—	—	—	—

* Dashes represent 0.

It has previously been observed that the long arm of the C^{K} is paired with the E^{X}. Therefore many of the CC=E trivalents depend upon pairing of the C^{K} and C^{X} short arms; although the C^{K} short arm is minute, it has been shown (above, p. 376) that chiasmata are formed in the C short arms in meiosis of *C. Kotschyana.*

The CC=E trivalent may be represented by the formula C^{XL}, C^{XS}-C^{KS}, $C^{KL}=E^{X}$ or C^{XS}, C^{XL}-$C^{KL}=E^{X}$ depending upon whether the C chromosomes are paired in their short or long arms.

AA=E.—It has previously been observed that in this trivalent one small chromosome is always paired with each end of the large chromosome, which has been identified as the A^{K}. Therefore the A^{K} is paired at one end with the A^{X} and at the other end with the E^{X} (pl. 19, fig. 2). It cannot be determined whether the E^{X} pairs with the A^{K} short or long arm. The chromosome arrangement of this trivalent is $A^{X}\text{-}A^{K}=E^{X}$.

AA=CC.—One of the C chromosomes is paired with the long A chromosome, therefore with the A^{K} (pl. 19, fig. 5). The probable arrangement is $A^{X}\text{-}A^{K}=C^{X}\text{-}C^{K}$. It cannot be determined from this configuration whether the A^{K} is paired with the short or the long arm of the C^{X}; however, it will be shown that in some AA=CC=E configurations the A^{K} and C^{XL} are paired.

AA=CC=E.—In the cells shown in plate 19, figures 6, 7, the D chromosomes are attached to the nucleolus, and the large nearly equal pair of B chromosomes is also easily identified. The pentavalent, therefore, is made up of the AA, CC, and E chromosomes. Considering only chromosome size and absence of autosyndesis, several interpretations of this pentavalent are possible. Final analysis depends upon the interpretation of the Y-shaped terminal part which may be made up of the C^{K} and C^{X} chromosomes (see pl. 19, fig. 1, *a*) or of the C^{K} and E^{X} chromosomes (see pl. 19, fig. 1, *b*). It is my opinion, based on the shape of the configuration, that the latter interpretation is correct; hence that the E^{X} and C^{K} chromosomes are involved in the terminal Y-shaped part of the pentavalent, and the short chromosome adjacent to the Y is not the E^{X} but the C^{X}, so that the following arrangement is probably correct: $A^{X}\text{-}A^{K}=C^{XL}$, $C^{XS}\text{-}C^{KS}$, $C^{KL}=E^{X}$.

Sometimes the AA=CC=E pentavalent appears as a linear configuration, with all the chiasmata terminalized or nearly terminalized. When the CC=E part of the pentavalent is in the form of a chain, the C chromosomes must be paired in their short arms, since the C^{KL} pairs with the E^{X}. In these pentavalents the chromosome arrangement may be either $A^{X}\text{-}A^{K}=C^{XL}$, $C^{XS}\text{-}C^{KS}$, $C^{KL}=E^{X}$ or $A^{X}\text{-}A^{K}=E^{X}=C^{KL}$, $C^{KS}\text{-}C^{XS}$, C^{XL}. However, both the CC=E and the AA=E trivalents are relatively frequent in occurrence in the hybrid cells; therefore the second of these arrangements, which allows both $C^{K}=E^{X}$ and $A^{K}=E^{X}$ pairing, seems the more probable.

BB=DD.—It may be observed in the quadrivalent shown in plate 20, figure 1, that the longer B chromosome, which is the B^{K}, is paired with the shorter D chromosome, which must be the D^{X}. Since the short, satellite-bearing arm of the D chromosome is in contact with the nucleolus, the chromosome arrangement must be $B^{X}\text{-}B^{K}=D^{XS}$, $D^{XL}\text{-}D^{KL}$, D^{KS}. In the BB=DD quadrivalent shown in plate 20, figure 2, the longer D (the D^{K}) is attached to the shorter B chromosome (B^{X}); it may be observed that the D chromosomes are paired in their long arms, since the short arm of one D chromosome is in contact with the nucleolus. Thus the arrangement is $B^{K}\text{-}B^{X}=D^{KS}$, $D^{KL}\text{-}D^{XL}$, D^{XS}.

DD=E.—The shorter D, which is the D^{X}, is attached to the nucleolus, presumably by its short arm, and the longer D, the D^{K}, is paired with the D^{X} long arm and attached by its short arm to the E^{X} chromosome (pl. 20, figs.

3, 8). Therefore the arrangement is D^{XS}, $D^{XL}\text{-}D^{KL}$, $D^{KS} = E^{X}$. In a few DD = E trivalents it was not possible to determine which arm of the D^{K} paired with the E^{X}.

DD = BB = E.—Assuming allosyndetic pairing, the E^{X} is attached to the B^{K}, which in turn is attached to the B^{X}, and that to the D^{K}, and that to the D^{X}, which is attached to the nucleolus by its short satellite arm (pl. 20, fig. 4). The arrangement of the chromosomes is: D^{XS}, $D^{XL}\text{-}D^{KL}$, $D^{KS} = B^{X}\text{-}B^{K} = E^{X}$.

BB = AA.—In this configuration (pl. 20, fig. 3), the long chromosome of the AA pair, the A^{K}, is paired with a B chromosome, which must therefore be the B^{X}. The chromosome arrangement is: $A^{X}\text{-}A^{K} = B^{X}\text{-}B^{K}$.

BB = AA = CC = E.—On the basis of chromosome size and allosyndetic pairing several different arrangements of the chromosomes of the septavalent shown in plate 20, figure 5 are possible. The final analysis of chromosome pairing here depends upon the interpretation of the terminal Y-shaped part of the septavalent, consisting of either the C^{K} and E^{X} or of the C^{K} and C^{X} chromosomes. In my opinion the arrangement of the CC = E chromosomes is like that shown in plate 19, figure 1, *b*, in which the Y is made up of the C^{K} and E^{X} chromosomes. Thus the chromosome arrangement of the septavalent is assumed to be: $B^{X}\text{-}B^{K} = A^{X}\text{-}A^{K} = C^{XL}$, $C^{XS}\text{-}C^{KS}$, $C^{KL} = E^{X}$.

DD = AA (or DD = A).—In several cells in which the configuration was observed one of the D chromosomes was attached to the nucleolus and the other D paired with the short member of the pair of A chromosomes, therefore with the A^{X}. It may be assumed that the satellite-bearing short arm of the D chromosome is associated with the nucleolus; thus the arrangement is probably: D^{XS}, $D^{XL}\text{-}D^{KL}$, $D^{KS} = A^{X}\text{-}A^{K}$. In several DD = AA quadrivalents the longer of the two A chromosomes is observed to be paired with a D chromosome. In these cases the chromosome arrangement is assumed to be: D^{KS}, $D^{KL}\text{-}D^{XL}$, $D^{XS} = A^{K}$, A^{X}.

BB = DD = AA.—In the cell shown in plate 20, figure 6, there is one univalent—the E chromosome, one bivalent—the CC chromosome pair, and a hexavalent, consisting of the BB, DD, and AA chromosomes. The A chromosomes are seen as the very unequal pair (the A^{K} seems to be somewhat stretched) at one end of the multivalent configuration. Attached to the long A^{K} is a D chromosome, which must therefore be the D^{X}. The D chromosome pair is attached to the almost equally sized large pair of chromosomes, the BB pair, and since the A^{K} is attached to the D^{X}, the B^{X} must be paired with the D^{K}. Thus the chromosome arrangement of this hexavalent is assumed to be: $B^{K}\text{-}B^{X} = D^{KS}$, $D^{KL}\text{-}D^{XL}$, $D^{XS} = A^{K}\text{-}A^{X}$.

Univalent chromosomes.—Although few unpaired regions were observed at pachytene, the members of certain pairs of chromosomes were not paired in each hybrid (table 5); it may be assumed either that the pachytene pairing involved these chromosomes in a non-homologous association, or that the association was homologous but no chiasmata were formed.

The A and C chromosomes were found to be unpaired much more frequently than members of the remaining chromosome pairs (pl. 20, fig. 9). The question arises whether lack of association of the A chromosomes is due to lack of homology between them, or whether it results in some way from the extreme reduction in size of the A^X. However, the reduction in size is common to the A chromosome of all the 5-paired species, whereas the percentage of cells in which the A chromosomes are not paired varies to a large extent in the different interspecific hybrids (table 5). It is probably correct to assume that the high percentage of unpaired A chromosomes in *Thomsonii* × *Kotschyana* indicates a larger proportion of non-homologous segments in the A chromosomes of these two species than is characteristic of the remaining species.

If a large portion of the C^K long arm is made up of material translocated from the E′ chromosome (and is therefore not homologous with the corresponding region of the 5-paired species) it is to be expected that a certain number of C chromosome univalents should appear in the hybrids. The C chromosome univalent frequency varies widely in the different hybrids. Evidently the material in the *C. Kotschyana* C chromosome, aside from that donated by the E′ chromosome, is closely homologous with that in the C chromosome of *C. foetida commutata* and *C. rubra,* but it is not entirely homologous with that in the C chromosomes of the remaining species (see table 5).

TABLE 5

PERCENTAGES OF VARIOUS UNIVALENT CHROMOSOMES AT DIAKINESIS IN THE SIX HYBRIDS

Hybrids	Chromosomes			
	A_I	B_I	C_I	D_I
Kotschyana × *alpina*	5	—*	6	2
Kotschyana × *syriaca*	9	1	17	6
Kotschyana × *rubra*	2	—	1	1
Eritreënsis × *Kotschyana*	6	—	18	—
Thomsonii × *Kotschyana*	22	4	19	8
Foetida commutata × *Kotschyana*	4	1	1	1

* Dashes represent 0.

In most of the hybrids the percentages of cells with unpaired B or D chromosomes is small (pl. 21, fig. 1). The degree of homology of the *C. Kotschyana* B and D chromosomes and those of the remaining species is probably relatively high.

ORIGIN OF TRANSLOCATIONS PRODUCING THESE CHROMOSOME ASSOCIATIONS

The question is now raised: which species has undergone the translocation which manifests itself in the hybrid as a multivalent association?

The associations between different non-homologous chromosomes of the six interspecific hybrids are arranged in table 6. This table has been compiled from the foregoing analyses of multivalent configurations in the diakinesis cells of the hybrids; only those associations which were observed in two or more hybrids are included. The *C. Kotschyana* chromosomes are indicated by the superior letter ^{K}, and chromosomes of the 5-paired species are indicated by

TABLE 6

FREQUENCY OF ASSOCIATIONS OF CHROMOSOME ARMS IN THE SIX HYBRIDS

(Percentage is shown in parentheses)

	$C^{KL}=E^{X}$	$A^{K}=E^{X}$*	$D^{KS}=E^{X}$	$D^{K}=E^{X}$	$B^{K}=E^{X}$	$A^{K}=B^{X}$	$A^{K}=C^{X}$	$A^{K}=C^{XL}$	$A^{K}=D^{X}$	$A^{K}=D^{XS}$	$B^{K}=D^{X}$	$B^{K}=D^{XS}$	$D^{KS}=B^{X}$
Kotschyana × *alpina*......	56 (41)	12 (9)	1 (1)	—†	1 (1)	1 (1)	—	—	—	—	—	2 (1)	—
Kotschyana × *syriaca*.....	30 (26)	15 (13)	—	3 (3)	—	—	—	1 (1)	3 (3)	2 (2)	—	1 (1)	1 (1)
Kotschyana × *rubra*......	72 (65)	17 (15)	2 (2)	—	—	—	—	5 (5)	—	—	—	6 (5)	—
Eritreënsis × *Kotschyana*.	13 (39)	1 (3)	1 (3)	—	—	1 (3)	—	1 (3)	—	—	—	—	2 (6)
Thomsonii × *Kotschyana*.	20 (20)	11 (11)	3 (3)	1 (1)	1 (1)	1 (1)	3 (3)	1 (1)	1 (1)	—	1 (1)	1 (1)	2 (2)
Foetida commutata × *Kotschyana*..........	62 (59)	5 (5)	1 (1)	—	—	—	5 (5)	6 (6)	1 (1)	3 (3)	—	8 (8)	1 (1)

* Probably more $A^{K}=E^{X}$ associations were present, since some AA=CC=E pentavalents could not be completely analyzed.

† Dashes represent 0.

the superior letter ^{X}. When it is known in which arm of the chromosome the chiasma lies, the information is added, but in some cases only the whole chromosome could be identified.

It is assumed that chromosome associations which are present in from four to six hybrids are the result of translocations which have occurred in *C. Kotschyana* or in its ancestral species, since it would demand too much of coincidence that the same translocation should occur in each 5-paired species. Conversely, a chromosome association which appears in only one or two hybrids may be assumed to have resulted from a translocation which took place in the 5-paired species, for had it occurred in *C. Kotschyana* it would be evident in at least the majority of the hybrids.

The first three chromosome associations in table 6 ($C^{KL}=E^X$, $A^K=E^X$, $D^{KS}=E^X$[6]), which are present in all six hybrids, corroborate the above assumption, for previous evidence has shown that the ancestral E′ chromosome was "lost" through translocation of segments to one or more of the remaining *C. Kotschyana* chromosomes.

Two chromosome associations are present in five hybrids: $A^K=C^{XL}$ and $B^K=D^{XS}$. Therefore these translocations must have occurred in the *C. Kotschyana* chromosomes; a segment of the long arm of the C^K translocated to the A^K and a segment of the short arm of the D^K translocated to the B^K. The $A^K=C^X$ association found in two hybrids may be the same $A^K=C^{XL}$ association which occurs in five of the six hybrids.

One chromosome association, $D^{KS}=B^X$, is present in four out of the six hybrids and probably represents the translocation of a segment of the *C. Kotschyana* B chromosome to the short arm of the *C. Kotschyana* D chromosome.

Two of the associations mentioned above, $B^K=D^{XS}$ and $D^{KS}=B^X$, appear at first glance to be evidence of a reciprocal translocation between the D^{KS} and the B^K, but inspection of the diakinesis figures suggests that these may actually be two separate translocations. In both plate 20, figure 1 ($B^K=D^{XS}$) and plate 20, figure 2 ($D^{KS}=B^X$) the quadrivalents are seen to be open-chain figures. It will be shown below that open-chain quadrivalents may be formed as a result of reciprocal translocation when one translocated segment is so small that no chiasma is formed in it; yet here chiasmata are formed between both the D^{XS} and B^K and the D^{KS} and B^X, and still no closed-ring quadrivalent was ever seen. Therefore this apparent reciprocal translocation probably represents two separate translocations.

The remaining translocations shown in table 6 are presumed to have occurred in the 5-paired species, based on the fact that they are found in three or fewer hybrids.

APPARENT ABSENCE OF RECIPROCAL TRANSLOCATION

The question is now raised: why no reciprocal translocations are shown in table 6, and why rings of chromosomes are not seen in diakinesis, but instead, multivalent configurations appear as open chains of 4 to 7 chromosomes (pl. 19, fig. 7; pl. 20, figs. 1, 6). This question does not refer to the *C. Kotschyana* associations with the E^{X}, naturally, since the E' chromosome was not maintained as an entity.

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[6] $D^{KS}=E^X$ probably includes $D^K=E^X$.

Investigations of *Crepis* have shown that the majority, if not all, of the translocations are reciprocal (Navashin and Gerassimova 1936, Lewitsky and Sizova 1935, and Korjukaev 1940). However, it has been shown that reciprocal translocations may involve segments of very unequal sizes. Thus, if it is assumed that translocations are generally reciprocal in *Crepis*, the open chains of chromosomes at diakinesis may be caused by one of the translocated segments being too small to form an association with its homologous segment in meiosis; this is especially probable in a genus such as *Crepis*, which is characterized by a relatively low chiasma frequency.

The formation of chains of four chromosomes has been observed in *Zea* by Burnham (1932) and Clarke and Anderson (1935) and in *Crepis* by Korjukaev (1940) and Tobgy (1943), and these investigators have concluded that such open chains of chromosomes are formed as a result of unequal reciprocal translocation involving segments of such unequal sizes that one segment is large enough to form an association which is maintained by the occurrence of a chiasma within it, whereas the other segment is so small that it either does not associate with its homologous segment at pachytene or that no chiasma is formed.

It is also possible that one of the two translocated segments may undergo further structural alterations and thus may lose its homology with the once corresponding segment in the *C. Kotschyana* set or in the chromosome sets of the 5-paired species.

FREQUENCIES OF DIFFERENT TYPES OF CHROMOSOME ASSOCIATIONS

The following six translocations have been shown to have occurred in *C. Kotschyana* or its ancestral species: $C^{KL}=E^{X}$; $A^{K}=E^{X}$; $D^{KS}=E^{X}$; $A^{K}=C^{XL}$; $B^{K}=D^{XS}$; $D^{KS}=B^{X}$.

It is obvious that of these the $C^{KL}=E^{X}$ chromosome association is by far the most frequently observed association in all six hybrids. The next most common chromosome association observed in each hybrid is the $A^{K}=E^{X}$, followed by the $A^{K}=C^{XL}$, $B^{K}=D^{XS}$, $D^{KS}=E^{X}$, and $D^{KS}=B^{X}$ associations. It is generally considered that within a hybrid the relative size of a heterozygous translocation is directly proportional to the relative frequency of the chromosome association brought about by that translocation: the larger the translocation the better chance of homologous pairing, and, once homologous pairing is accomplished, the greater the number of chiasmata formed within the translocation region. Therefore it may be concluded that the $E=C$ translocation is by far the largest, the $E=A$ translocation is much smaller, and the $A=C$, $B=D$, $D=E$, and $D=B$ translocations are still smaller.

It is possible that the translocation between the E' and the long arm of the C^{K} included most of one arm of the E'. Thus it may be suggested that the translocation between the E' and the A^{K} and between the E' and the D^{KS} involved the other arm of the E' chromosome. The remaining translocations shown in table 6, which have taken place in the chromosomes of the 5-paired species, are assumed to be very small, since such associations appear in 3 per cent of the cells or fewer.

Three translocations involving the E′ chromosome have been shown to have occurred in the ancestor of *C. Kotschyana:* $C^{KL}=E^{X}$; $A^{K}=E^{X}$; $D^{KS}=E^{X}$. It may be observed in table 6 that there is variation in the proportion of cells exhibiting each one of these chromosome associations in the different hybrids. For example, the proportion of cells exhibiting the $C^{KL}=E^{X}$ association ranges from 65 per cent in *Kotschyana* × *rubra* to 20 per cent in *Thomsonii* × *Kotschyana*, and the percentage of cells bearing the $A^{K}=E^{X}$ association ranges from 15 per cent (*Kotschyana* × *rubra*) to 3 per cent (*eritreënsis* × *Kotschyana*). What is the reason for this variation?

It has been suggested that combination of genetic factors in each hybrid determines the chiasma frequency, which in turn determines the amount of pairing, multivalent frequency, and univalent frequency. If this is so, the above-mentioned differences in chromosome associations exhibited by each hybrid may be simply an expression of genetically controlled differences in chiasma frequency and terminalization.

However, it has been found that although there is an almost direct correlation between chiasma frequency in each hybrid and the frequency of the $C^{KL}=E^{X}$ association, there is no correlation between chiasma frequency and the frequency of the $A^{K}=E^{X}$ association. Thus it is believed that the basis of a difference between interspecific hybrids in frequency of a certain chromosome association is not primarily caused by the variation in chiasma frequency but is caused instead by differences in chromosome structure which are expressed in spite of differences in chiasma frequency. The most probable explanation of the differences in percentage of cells possessing the same association in the different hybrids is that they are caused by variation in the size of the homologous segments involved in the association. Since the *C. Kotschyana* set is a constant factor in each hybrid, the above-mentioned variation in size of homologous translocated segments must lie in the chromosomes of the 5-paired species.

TERMINALIZATION OF CHIASMATA IN THE SIX HYBRIDS

There are indications that in these interspecific hybrids terminalization through non-homologous regions may occur. In spite of the fact that hybrid diakinesis multivalent configurations indicate the presence of non-homologous segments in homologous chromosomes of the parent species, the terminalization coefficients of hybrid diakinesis cells are actually higher than the terminalization coefficients of the parent species (table 3).

Furthermore, evidence of terminalization through non-homologous regions may be obtained from the following chromosome configurations:

1. The presence of a segment of the E′ chromosome in the long arm of the C^{K} has been demonstrated (above, p. 379). In the hybrids the C chromosomes are almost invariably paired in one arm only. In approximately 45 per cent of the hybrid diakinesis cells in which the C chromosomes are present as a pair, the chiasma (usually there is only one) is completely terminalized. When the minute size of the C^{K} short arm is taken into consideration (see above, p. 376),

it seems reasonable to assume that in the majority of C chromosome pairs the chiasmata are formed in the long arms.

2. It has been shown that the A^K and E^X conjugate, as well as the A^K and C^{XL}, and it has been assumed from this that a segment of the E′ chromosome is situated in the A^K and that a segment of the C^{XL} is situated in the A^K (see above, pp. 381–383). However, in 13 per cent of the hybrid diakinesis cells the A chromosomes are paired in their long and short arms and both chiasmata are terminalized (pl. 20, figs. 1, 4).

3. In plate 20, figure 7, an AA=E trivalent is shown in which all three chiasmata are terminalized. One of these chiasmata must have terminalized through a non-homologous region. Similarly, in the CC=E trivalent shown in plate 19, figure 1, *i*, all three chiasmata are terminalized; one of the chiasmata must have terminalized through a non-homologous region.

TABLE 7

Frequency of Inversion Bridges in First and Second Anaphase of the Six Interspecific Hybrids

Interspecific Hybrids	Anaphase I			Anaphase II		
	One bridge	Two bridges	Total bridges	One bridge	Two bridges	Total bridges
Thomsonii × *Kotschyana*..........	36	6	47	14	2	18
Eritreënsis × *Kotschyana*..........	35	3 (1=3br)	42	15	2	19
Foetida commutata × *Kotschyana*...	41	7	55	27	4	35
Kotschyana × *rubra*..............	22	6 (1=3br)	35	22	11 (1=4br)	46
Kotschyana × *syriaca*.............	35	5	45	9	3	15
Kotschyana × *alpina*..............	20	1	22	20	9	38

The material was not suitable for an extensive study of terminalization in the interspecific hybrids, since metaphase chromosomes could not always be identified. From the material presented, however, it will be seen that there is evidence that in these interspecific hybrids terminalization past non-homologous regions can take place.

METAPHASE, ANAPHASE, AND TELOPHASE

Metaphase was studied and configurations were found ranging in type from 9_{I} to $1_{VII}+1_{II}$. Several metaphase configurations are shown in plate 21, figures 2–11. The material was not suitable for a detailed investigation of this stage.

In anaphase-telophase there is evidence of another type of structural hybridity in the appearance of the dicentric chromatid bridge accompanied by an acentric fragment, which is indicative of the presence of a heterozygous inversion in the hybrid.

In each hybrid 100 first anaphase-telophase cells and 100 second anaphase-telophase cells were examined and the data collected are arranged in table 7. It may be seen that most frequently only one bridge per cell was found; relatively few cells contained two or more bridges. The majority of the first anaphase bridges were broken at first telophase. However, a few persisting bridges were seen at telophase and these formed some of the second anaphase bridges.

Because there is evidence that the degree of contraction of fragments may be extremely variable in acetic-alcohol fixatives (Swanson, 1940), no analysis of fragment sizes was made; the study was conducted from the point of view of bridge frequency alone. It was found that the total number of first division bridges per 100 cells ranges from 22 to 55 in the six hybrids, and the total number of second division bridges per 100 cells ranges from 15 to 46.

The relatively large number of bridges observed at first and second anaphase-telophase indicates the presence in each hybrid of at least several heterozygous inversions.

CONCLUSION AND SUMMARY

It is known that the aneuploid decrease of chromosome number of the species within a genus has been a very widespread evolutionary phenomenon. Therefore the mechanism of such changes in chromosome number is a problem of interest and importance. A possible method of aneuploid changes in chromosome number was advanced by Navashin (1932) and Navashin and Gerassimova (1936) as the dislocation hypothesis, according to which decrease in chromosome number results from the occurrence of unequal reciprocal translocations which transfer the genetic material of one chromosome to one or more other chromosomes of the set, followed by loss of the centromere bearing no genetically active material, and finally, by the origin of an individual homozygous for the new karyotype. It is also possible that hybridization of strains with complementary translocations followed by elimination of the extra centromeres and duplicated material may produce a new karyotype which has one less pair of chromosomes but which possesses the same structural elements which were present in the former karyotype.

In the genus *Crepis* the decrease in basic chromosome number, which has produced an aneuploid series, may be said to be the outstanding feature of karyotype evolution. There are several closely related groups of species in which decrease in chromosome number has occurred and in which the chromosomes are distinct enough to be identified in postpachytene stages. Investigations of meiosis in F_1 hybrids between such related species with different chromosome numbers make it possible to identify translocations expected on the basis of the above hypotheses and thus to provide a cytological demonstration of the processes involved in the decrease in chromosome number as they have occurred in nature. This investigation of such a group of *Crepis* species and their interspecific hybrids was undertaken for this purpose.

The group of species studied were *C. Kotschyana* ($n=4$) and *C. Thomsonii*, *C. eritreënsis*, *C. foetida commutata*, *C. rubra*, *C. syriaca*, and *C. alpina* (all with $n=5$). *C. Kotschyana* has been included in the group of 5-paired species on the basis of morphological similarity and geographical distribution and it has been concluded, from the taxonomic position of *C. Kotschyana* in relation to the 5-paired species, that its 4-paired chromosome set represents a decrease in chromosome number from an ancestral 5-paired set. Following Navashin's terminology, the chromosomes of the 5-paired species are designated A, B, C, D, and E chromosomes. Comparison of the *C. Kotschyana* karyotype with those of the 5-paired species shows that its A, B, C, and D chromosomes are very much like the corresponding chromosomes of the 5-paired species but that there is no E chromosome in the *C. Kotschyana* complement (pl. 16).

The specific aim of this investigation, then, was to determine whether evidence could be obtained of a series of translocations of the ancestral *C. Kotschyana* E chromosome (designated E′) to one or more other chromosomes of the set, thus providing a demonstration of the processes involved in the decrease in chromosome number as they have occurred in the evolution of *C. Kotschyana.*

If segments of the E′ have been translocated to one or several of the remaining chromosomes of the set, these translocations will be present in the heterozygous condition in hybrids of *C. Kotschyana* with the 5-paired species, and will manifest themselves as multivalent associations in meiosis of the hybrids. Since the chromosome pairs and, in many cases the individual chromosomes, can be identified in diakinesis of the interspecific hybrids, it should be possible to determine, in part at least, to which chromosome or chromosomes of the *C. Kotschyana* (ancestral) set portions of the E′ chromosome were translocated.

Furthermore, it is generally considered that within a hybrid the relative size of a heterozygous translocation is directly proportional to the relative frequency of the appearance of the chromosome association brought about by the translocation. Therefore it is possible to obtain an estimate of the size of the translocated segments.

Through analysis of the multivalent configurations observed in diakinesis of the interspecific hybrids, three chromosome associations involving the E chromosome of the 5-paired parent (E^{X}) with a *C. Kotschyana* chromosome were found; these were the following: $C^{KL} = E^{X}$, $A^{K} = E^{X}$, $D^{KS} = E^{X}$. The $C^{KL} = E^{X}$ is by far the most frequently observed association in all six hybrids, occurring in from 65 per cent to 20 per cent of the diakinesis cells; the $A^{K} = E^{X}$ was the next most common association, occurring in from 15 per cent to 3 per cent of the hybrid diakinesis cells; the $D^{KS} = E^{X}$ association was observed in comparatively few cells.

From the frequency with which the C = E association is observed, it may be concluded that the translocated segment of E′ chromosome was relatively large, possibly including an entire arm. It has been shown that the short arm of the *C. Kotschyana* C chromosome is minute. Therefore the conclusion is reached that a large segment of the E′ chromosome was translocated to the long arm of the *C. Kotschyana* C chromosome.

The segment of E′ chromosome which translocated to the A^{K} must have been considerably smaller than that translocated to the C^{KL}, and the segment of E′ chromosome which was translocated to the D^{KS} was still smaller. It is probable that the translocation between the E′ and the long arm of the C^{K}

included most of one arm of the E′; therefore it may be suggested that the translocation between the E′ and the A^K and that between the E′ and the D^{KS} involved the other arm of the E′ chromosome.

It has been demonstrated that most if not all translocations in *Crepis* are reciprocal. However, in order for the E′ chromosome centromere to be eliminated without fatal results, the translocations involving the E′ chromosome must have been very unequal, so that eventually none or a minute amount of genetically active material was attached to the E′ centromere. There is evidence that the translocations involving the E′ chromosome were exceedingly unequal, for no rings of chromosomes were ever seen in diakinesis of these interspecific hybrids, but instead multivalent configurations appeared as open chains. It has been concluded by other investigators that such open chains of chromosomes are formed as a result of reciprocal translocation involving segments of such unequal sizes that one segment is large enough to form an association which is maintained by the occurrence of a chiasma within it, whereas the other segment is so small that it either does not associate with its homologous segment at pachytene or that no chiasma is formed.

Thus it has been shown that in the evolution of *C. Kotschyana* a series of three translocations have occurred which have transferred material of the E′ chromosome to three other chromosomes of the set. The E=C translocation involved a very large segment, possibly an entire arm, of the E′ chromosome; the smaller E=A and E=D translocations probably involved the second arm of the E′. It is concluded that these three translocations removed all or nearly all of the genetically active material of the E′ chromosome to the A, C, and D chromosomes so that the 4-paired *C. Kotschyana* set is genetically comparable with the ancestral 5-paired set. It may be noted in this connection that the *C. Kotschyana* somatic chromosomes are longer than those of the 5-paired species; this is particularly true of the long arm of the C^K, which, according to the above analysis, has received the largest segment of E′ chromosome. It also may be pointed out that the A and C chromosomes were unpaired much more frequently than the members of the remaining chromosome pairs in diakinesis of the hybrids. This is to be expected if the A^K and C^K contain segments of the E′, which have no homologues in the A^X and C^X.

It is possible that hybridization may have played a part in producing the 4-paired *C. Kotschyana*. For example, the E=A and E=D translocations may have taken place in one strain of the *C. Kotschyana* ancestor, removing, say, arm 1 of the E′ chromosome to these other chromosomes; in a second strain of *C. Kotschyana* the E=C translocation may have transferred arm 2 of the E′ chromosome to the C chromosome. If these two strains should hybridize, and the two E′ centromeres with attached arms 1 and 2 be lost, the resulting karyotype would have four pairs of chromosomes but would contain the same structural elements which were present in the original karyotype.

It is also possible that the translocations may have occurred in succession in one strain of the *C. Kotschyana* ancestral species, as suggested by Navashin's dislocation hypothesis.

The aim of this investigation was to determine whether the basic postulate of both hypotheses, that is, a series of translocations transferring the genetic material of one chromosome to one or more other chromosomes of the set, could be demonstrated to have occurred in nature in the evolution of a species with a decreased chromosome number. It has been demonstrated that such a series of translocations has occurred during the course of the evolution of *C. Kotschyana* from a 5-paired ancestor. This paper is summarized as follows:

1. The present investigation of the interspecific hybrids between six 5-paired species of *Crepis* and the 4-paired species *C. Kotschyana,* which has evolved from a 5-paired ancestor, was undertaken in order to determine the processes involved in the decrease of chromosome number.

2. The karyotypes of the seven species show considerable similarity. The *C. Kotschyana* complement, however, lacks the E chromosome present in the 5-paired species. The individual chromosomes of *C. Kotschyana* are longer than the corresponding chromosomes of the 5-paired species.

3. In diakinesis of the parent species the chromosomes form every type of bivalent possible, with chiasma frequencies ranging from 1 to 4 per bivalent. Chiasmata are not localized, but appear in terminal as well as interstitial positions, suggesting that chiasma formation is initiated at random.

4. It was concluded that almost all the quantitative and qualitative characters measured in the interspecific hybrids, which are to a large extent those differentiating the species in this group, are controlled by several or many pairs of factors as well as by accessory factors which may exert a modifying or inhibiting influence.

5. Differential amphiplasty, that is, non-appearance of the satellite of the D chromosome of one or both sets, was observed in mitosis of some of these hybrids and attributed to genetic causes.

6. The somatic chromosome complements of the 5-paired species range from 108 per cent to 88 per cent as long as the *C. Kotschyana* complement. It was therefore surprising to find that in pachytene of the hybrids chromosome ends are generally paired and that there is a high degree of pairing of the hybrid chromosomes throughout their lengths.

7. In diakinesis of *C. Kotschyana* there are four large and four small chromosomes, and in diakinesis of the 5-paired species four large and six small chromosomes are present. However, diakinesis cells of all six hybrids exhibit three large chromosomes and six small chromosomes. On the basis of comparative somatic chromosome morphology and allosyndetic pairing in multivalent configurations, it was concluded that the unexpected small chromosome observed in meiosis of the hybrids is the A^x, which had decreased approximately one-half in length. No change in the width of this chromosome was observed.

8. Various multivalent configurations were observed in diakinesis of the six interspecific hybrids, ranging from relatively common trivalents to rare hexavalent and septavalent associations. The most common multivalent configuration in each hybrid was the CC=E trivalent, followed by the AA=E, AA=CC=E, and BB=DD multivalents.

9. Although few unpaired regions were observed at pachytene, the members of certain pairs of chromosomes were found to be unpaired at diakinesis and

later meiotic stages. The A and C chromosomes exhibit the highest degree of univalent formation.

10. Six translocations were shown to have occurred in *C. Kotschyana* or its ancestor, and several very small translocations were shown to have occurred in the 5-paired species. Of the six translocations which must have occurred in the 5-paired ancestor of *C. Kotschyana,* three involved the E′ chromosome. The C=E association was present in a very large proportion of the hybrid diakinesis cells, the A=E association was present in a smaller proportion of the hybrid cells, and the D=E association was observed in relatively few cells. Since the size of a translocation is generally considered to be proportional to the frequency of the appearance of the corresponding chromosome association, it is concluded that a large segment of the E′ chromosome, perhaps an entire arm, translocated to the C^K; the translocation must have involved the long arm of the C^K, for the short arm of this chromosome is minute. The A=E and D=E translocations were smaller, and probably involved the other arm of the E′ chromosome.

11. Several types of CC=E configurations were observed. Pairing must have occurred between various regions of the C^{KL} and the E^X, indicating that there has been rearrangement of the E′ material in the C^{KL} following the initial translocation.

12. Multivalents were never found as rings of chromosomes, but always appeared as open chains. It was concluded that this was caused by unequal reciprocal translocation, one segment being so small that it either did not associate with its homologue or that no chiasma was formed.

13. There is variation in the proportion of cells exhibiting each chromosome association in the different hybrids. This is attributed to variation in the size of the homologous segments involved in the association. These differences must lie in the chromosomes of the 5-paired species, since the *C. Kotschyana* set is a constant factor in each hybrid.

14. There is some evidence, obtained from comparing the terminalization coefficients of parents and hybrids and from certain chromosome associations, that in these hybrids terminalization through non-homologous regions occurs.

15. It is concluded that the decrease in chromosome number in *C. Kotschyana* was brought about by translocations which transferred the genetically active material of the E′ chromosome to the A, C, and D chromosomes of the ancestral *C. Kotschyana* set. It is possible that these translocations took place successively in one strain of the *C. Kotschyana* ancestor and that the 4-paired species was established following loss of the free centromere, or that the translocations took place independently in two separate strains of the *C. Kotschyana* ancestor, followed by hybridization of the two complementary types, and by elimination of the extra centromere and attached duplicated material. The basic postulate of both hypotheses, that is, a series of translocations transferring the genetic material of the small, medianly constricted E′ chromosome to other chromosomes of the set, has now been shown to have occurred in nature in the evolution of the 4-paired *C. Kotschyana* from a 5-paired ancestor.

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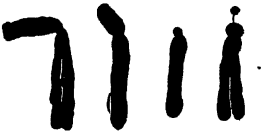
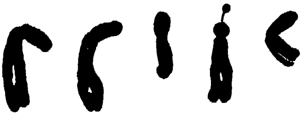
PLATES

PLATE 16

Somatic chromosomes, haploid set, of the seven species of *Crepis*.



KOTSCHYANA



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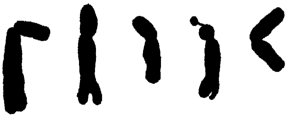

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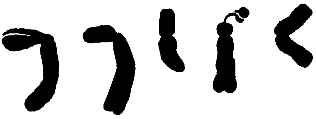

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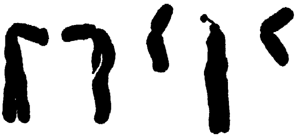

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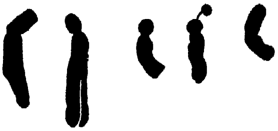

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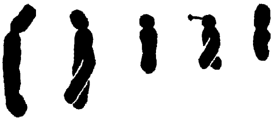
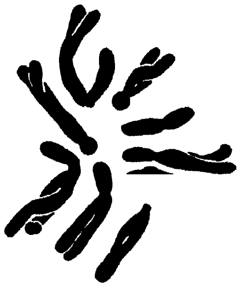


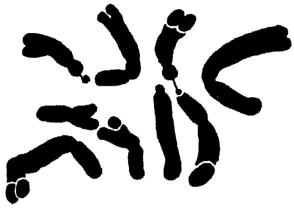
ALPINA

PLATE 17

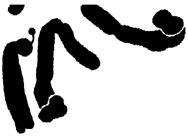
Somatic chromosomes, diploid set, of the six interspecific hybrids.



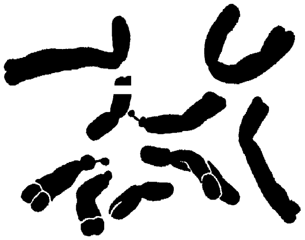
Thomsonii x Kotschyana



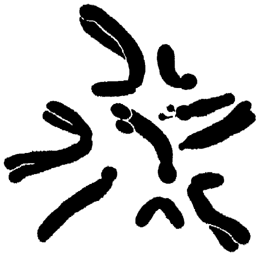
eritreensis x Kotschyana



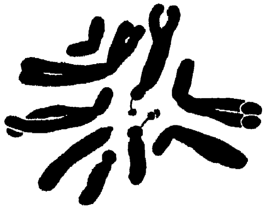
foetida commutata x Kotschyana



Kotschyana x rubra



Kotschyana x syriaca



Kotschyana x alpina

PLATE 18

Meiosis in the parent species and the interspecific hybrids.

Fig. 1. Pachytene cells of the *Kotschyana* × *rubra* hybrid.

Fig. 2. Pachytene cell of the *foetida commutata* × *Kotschyana* hybrid.

Fig. 3. Diakinesis cell of *C. Kotschyana* ($n = 4$).

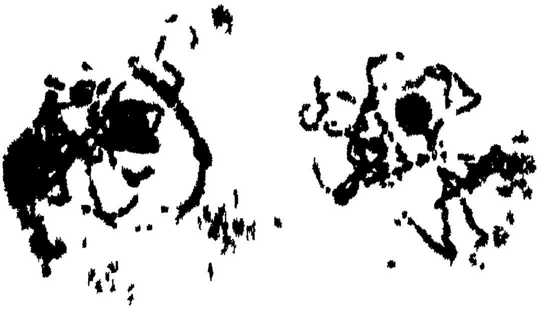
Fig. 4. Diakinesis cell of *C. rubra* ($n = 5$).

Fig. 5. Diakinesis cell of *C. syriaca* ($n = 5$).

Fig. 6. Diakinesis cell of the *Kotschyana* × *rubra* hybrid (note 3 large and 6 small chromosomes).

Fig. 7. Diakinesis cell of the *Kotschyana* × *syriaca* hybrid (3 large and 6 small chromosomes).

Fig. 8. Diakinesis cell of the *Kotschyana* × *syriaca* hybrid (4 large and 5 small chromosomes). The cells shown in figures 7 and 8 were found on the same slide.



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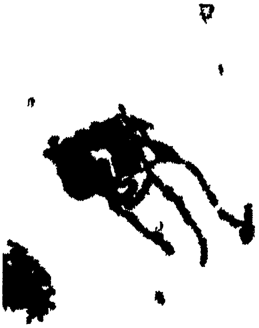

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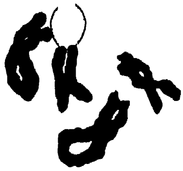

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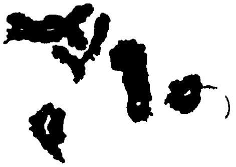

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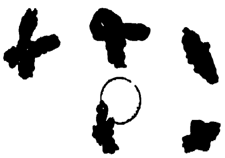

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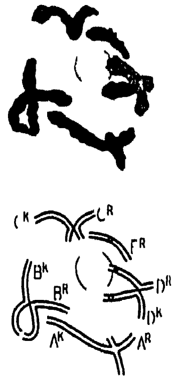

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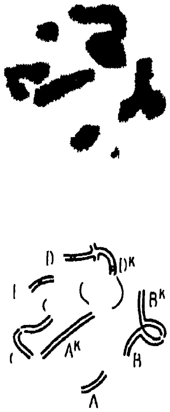

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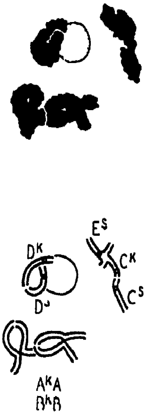


8

PLATE 19

Meiosis in the interspecific hybrids.

Fig. 1. Various types of $CC = E$ trivalents which were observed in diakinesis of the six interspecific hybrids.

Fig. 2. Diakinesis cell of the *Thomsonii* × *Kotschyana* hybrid, containing $3_{II} + 1_{III}$—the trivalent is $A^{T}\text{-}A^{K} = E^{T}$.

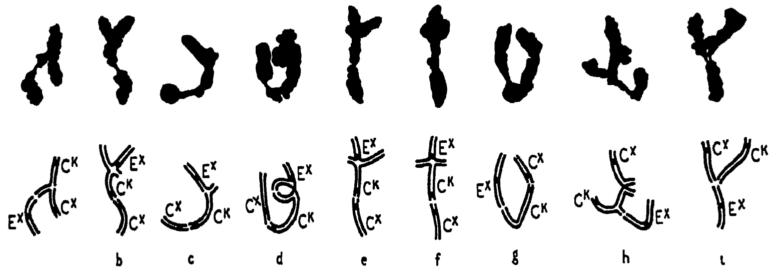
Fig. 3. Diakinesis cell of the *Thomsonii* × *Kotschyana* hybrid, containing $1_{II} + 2_{III} + 1_{I}$—the trivalents are $B^{T}\text{-}B^{K} = D^{T}$ and C^{TL}, $C^{TS}\text{-}C^{KS}$, $C^{KL} = E^{T}$.

Fig. 4. Diakinesis cell of the *Thomsonii* × *Kotschyana* hybrid, containing $3_{II} + 1_{III}$—the trivalent is C^{TS}, $C^{TL}\text{-}C^{KL} = E^{T}$.

Fig. 5. Diakinesis cell of the *Thomsonii* × *Kotschyana* hybrid, containing $2_{II} + 1_{IV} + 1_{I}$—the quadrivalent is $A^{T}\text{-}A^{K} = C^{T}\text{-}C^{K}$.

Fig. 6. Diakinesis cell of the *Thomsonii* × *Kotschyana* hybrid, containing $2_{II} + 1_{V}$—the pentavalent is $A^{T}\text{-}A^{K} = C^{TL}$, $C^{TS}\text{-}C^{KS}$, $C^{KL} = E^{T}$.

Fig. 7. Diakinesis cell of the *foetida commutata* × *Kotschyana* hybrid, containing $2_{II} + 1_{V}$—the pentavalent is $A^{F}\text{-}A^{K} = C^{FL}$, $C^{FS}\text{-}C^{KS}$, $C^{KL} = E^{F}$.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E^X
C^X
E^X
C^K
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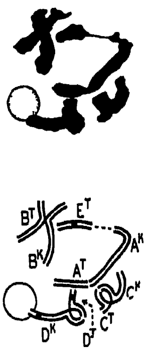
e
f
g
h
i

1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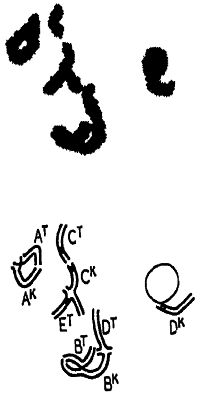
A^K
B^K
A^T
C^K
D^K
D^T
C^T

2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A^K
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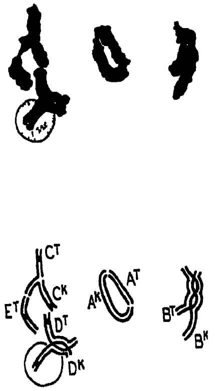
B^K
D^K

3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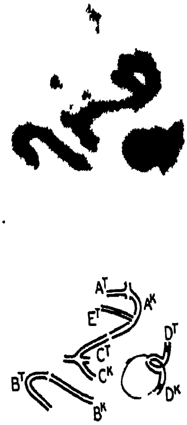
D^K

4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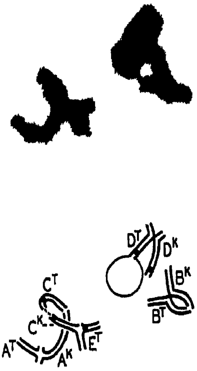
D^K

5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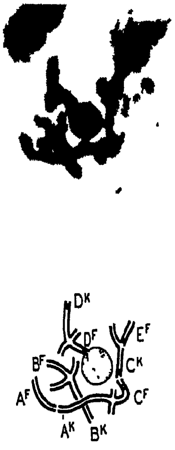
A^T
A^K
E^T

6


D^K
D^F
E^F
B^F
C^K
A^F
C^F
A^K
B^K

7

PLATE 20

Meiosis in the interspecific hybrids.

Fig. 1. Diakinesis cell of the *Thomsonii* × *Kotschyana* hybrid, containing $2_{II}+1_{IV}+1_{I}$ the quadrivalent is B^{T}-$B^{K}=D^{TS}$, D^{TL}-D^{KL}, D^{KS}.

Fig. 2. Diakinesis cell of the *Thomsonii* × *Kotschyana* hybrid, containing $2_{II}+1_{IV}+1_{I}$ the quadrivalent is B^{K}-$B^{T}=D^{KS}$, D^{KL}-D^{TL}, D^{TS}.

Fig. 3. Diakinesis cell of the *Kotschyana* × *eritreensis* hybrid, containing $1_{III}+1_{IV}+2_{I}$—the trivalent is D^{ES}, D^{EL}-D^{KL}, $D^{KS}=E^{E}$ and the quadrivalent is A^{E}-$A^{K}=B^{E}$-B^{K}.

Fig. 4. Diakinesis cell of the *Thomsonii* × *Kotschyana* hybrid, containing $2_{II}+1_{V}$—the pentavalent is D^{TS}, D^{TL}-D^{KL}, $D^{KS}=B^{T}$-$B^{K}=E^{T}$.

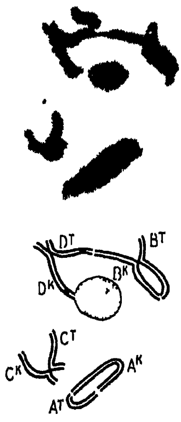
Fig. 5. Diakinesis cell of the *foetida commutata* × *Kotschyana* hybrid, containing $1_{II}+1_{VII}$--the septavalent is B^{F}-$B^{K}=A^{F}$-$A^{K}=C^{FL}$, C^{FS}-C^{KS}, $C^{KL}=E^{F}$.

Fig. 6. Diakinesis cell of the *foetida commutata* × *Kotschyana* hybrid, containing $1_{II}+1_{VI}+1_{I}$ -the hexavalent is B^{K}-$B^{F}=D^{KS}$, D^{KL}-D^{FL}, $D^{FS}=A^{K}$-A^{F}.

Fig. 7. Diakinesis cell of the *Kotschyana* × *rubra* hybrid, containing a $CC'=E$ trivalent in the form of a "frying pan" configuration; note that the chiasmata are completely terminalized.

Fig. 8. Diakinesis cell of the *Thomsonii* × *Kotschyana* hybrid, containing $3_{II}+1_{III}$—the trivalent is D^{TS}, D^{TL}-D^{KL}, $D^{KS}=E^{T}$.

Fig. 9. Diakinesis cell of the *Thomsonii* × *Kotschyana* hybrid, containing $2_{II}+5_{I}$; the A and C chromosomes are present as univalents. Note the difference in size between the A^{K} and the A^{T}.


DT
BT
DK
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CT
CK
AK
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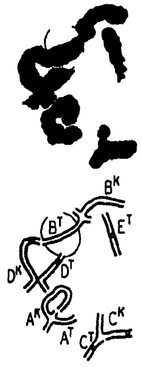
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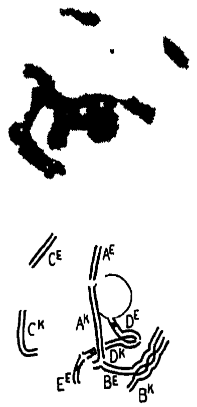
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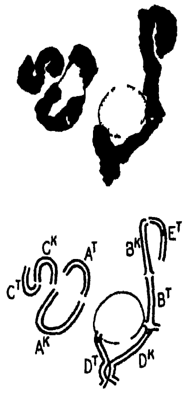
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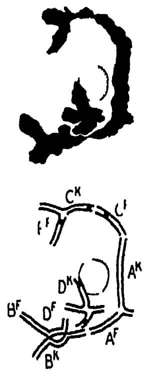
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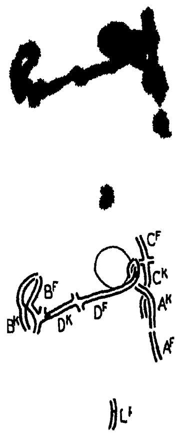
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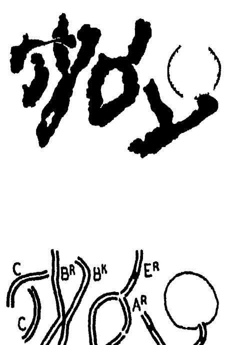
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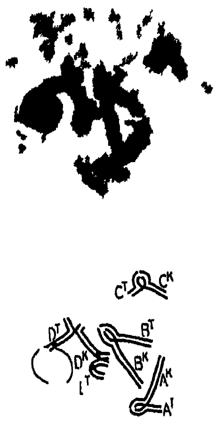
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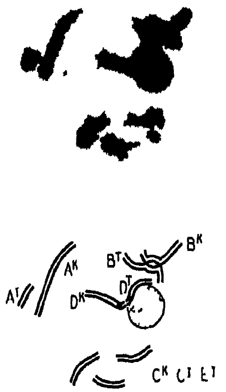
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PLATE 21

Meiosis in the interspecific hybrids.

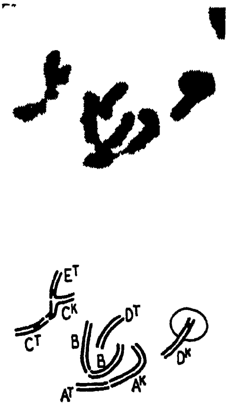
Fig. 1. Diakinesis cell of the *Thomsonii* × *Kotschyana* hybrid, containing $2_{II}+1_{III}+2_{I}$—the trivalent is made up of the CC=E chromosomes and the univalent chromosomes are the D^{T} and the D^{K}.

Fig. 2. Metaphase cell of the *eritreënsis* × *Kotschyana* hybrid; note the difference in size of the chromosomes of the unequal pair and also the fact that the short arm of the long chromosome of the unequal pair is longer than the short arm of either chromosome of the large nearly equal pair.

Fig. 3. Metaphase cell of the *Kotschyana* × *rubra* hybrid, containing $2_{II}+1_{V}$—the pentavalent is A^{R}-A^{KL}, $A^{KS}=E^{R}=C^{KL}$-C^{RL}, C^{RS}.

Fig. 4. Metaphase cell of the *Thomsonii* × *Kotschyana* hybrid, containing $4_{II}+1_{I}$; note that the short arm of the large chromosome of the unequal pair is longer than the short arm of either chromosome of the large nearly equal pair.

Figs. 5–11. Metaphase cells of various interspecific hybrids, containing the following configurations: $3_{II}+2_{I}$; $3_{II}+1_{III}$; $2_{II}+1_{IV}+1_{I}$; $2_{II}+1_{III}+2_{I}$; $3_{II}+1_{III}$; $2_{II}+1_{III}+2_{I}$; $2_{IV}+1_{I}$.



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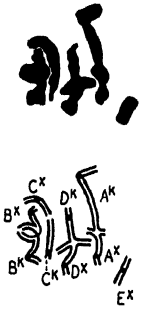

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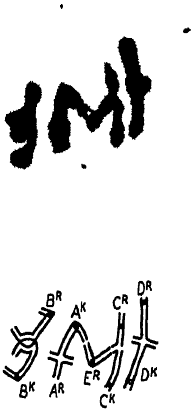

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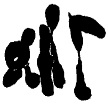

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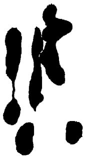

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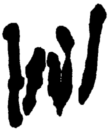

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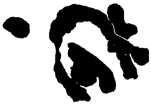

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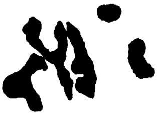

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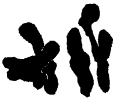

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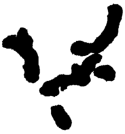

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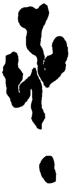

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HAWAIIAN REPRESENTATIVES OF THE GENUS CAULERPA

BY

LOIS L. EUBANK

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HAWAIIAN REPRESENTATIVES OF THE GENUS CAULERPA

BY

LOIS L. EUBANK

ALTHOUGH the Hawaiian Archipelago has been known to the world of science since its discovery by Captain Cook in 1778, little work has been done on the marine algae of the region. A few publications may be mentioned as representative of the present state of knowledge, but on the whole they are little more than obsolete lists of some of the commoner seaweeds: Chamberlain (1880) recorded 112 species; Tilden (1901) listed less than 100 forms; Lemmermann (1905) included in his paper approximately 70 species based upon material collected by Shauinsland and upon the records of some of the earlier writers, such as Dickie (1876, 1877), De Toni (1889), Reinbold (1899) and others; Reed (1907) listed some 50 economic seaweeds; Rock (1913) published a catalogue which was an expansion of Reed's list; MacCaughey (1918) in addition to recording 115 species (compiled in part from the lists of Lemmermann and others), added notes of an ecological nature; Neal (1930) published the results of some successional studies of marine algae and gave an annotated list of 60 plants; and Howe (1934) gave an account, including the description of a few new species, of a small collection brought home by Galtsoff. Several additional references might be added, but knowledge of the flora is based primarily upon the papers cited above.

While at the University of Hawaii during 1941–1942, I undertook a study of certain Hawaiian marine algae. Collections were made on the Island of Oahu over a period of ten months. The present account is based on a study of the material of *Caulerpa* collected at that time, as well as that in the collections of Papenfuss, Reed, Rock, and Setchell which are deposited in the herbarium of the University of California.[*]

Previous records of *Caulerpa* in Hawaii included but eight names: *C. Chemnitzia* (Chamberlain, 1880), *C. clavifera* (Chamberlain, 1880), *C. asplenioides* (Chamberlain, 1880), *C. taxifolia* (Chamberlain, 1880; Tilden, 1901; MacCaughey, 1918), *C. pinnata* (Lemmermann, 1905; MacCaughey, 1918), *C. racemosa* var. *laetevirens* (Lemmermann, 1905; MacCaughey, 1918), *C. Pickeringii* (Neal, 1930), and *C. serrulata* (Howe, 1934). Their present status is discussed in this paper, along with an expansion of the list to include several new records for the Archipelago.

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[*] This research was made possible by a fellowship from the Fiftieth Anniversary Thanksgiving Fund of Delta Delta Delta Sorority. The writer wishes to express appreciation for the use of the excellent algological library of the late Professor William A. Setchell at the University of California. Mr. T. T. McCabe kindly prepared the photographs and checked the Latin descriptions. The investigation has been carried out under the supervision of Dr. George F. Papenfuss, to whom many thanks are due for generously giving of his time to discussing the problems that arose throughout the study.

GENUS CAULERPA

Caulerpa Lamouroux 1809, p. 136.

Thallus nonseptate, coenocytic, from 2 mm. to a meter in length, differentiated into a prostrate, branched rhizome and erect assimilative fronds, which usually consist of an axis beset with ramuli of diverse form; internally thallus traversed by trabeculae, which are extensions of the cell wall; reproduction vegetative and sexual, the latter anisogamous; gametes are liberated through papillae that develop on the frond, or occasionally on the rhizome.

Caulerpa is a genus exhibiting a high degree of polymorphism. In Hawaii, this is best exemplified by *C. ambigua, C. serrulata,* and *C. racemosa.* Before such a group can be attacked from the genetic, physiologic, or ecologic viewpoint, a taxonomic organization of the material seems an essential starting point. Whether the plasticity demonstrated by the species is due to a high genetic diversity within the population, to the effect of ecological factors, or to an interacting of both in the isolation of ecotypes, is not yet understood. Tandy (1934, p. 63) who has done some experimental culturing of members of the genus says, "The characters relied on for [specific] separations [within the genus] can be varied by transplant experiments on a single ramulus... There is evidence that *C. peltata* Lamx. and *C. fastigiata* Mont. are only forms of *C. racemosa.*" Accordingly, we must admit that the boundaries which delimit certain "species" of *Caulerpa,* and the categories within such species, are undefinable at present.

KEY TO HAWAIIAN SPECIES

1. Fronds lacking ramuli...5. *C. serrulata*
1. Fronds beset with ramuli...(2)
    2. Ramuli differentiated into pedicel and inflated apex...(3)
    2. Ramuli not pedicellate; filiform or tapering toward apex...(4)
3. Ramuli with constriction between pedicel and globose apex............6. *C. lentillifera*
3. Ramuli lacking constriction, apex globose to plano-convex...............7. *C. racemosa*
    4. Ramuli distinctly mucronate...(5)
    4. Ramuli obtuse to acuminate, rarely, if at all, mucronate...(6)
5. Ramuli distichously arranged, simple, laterally compressed, sickle-shaped..4. *C. taxifolia*
5. Ramuli verticillately arranged, furcate, terete.........................2. *C. Webbiana*
    6. Plant minute, 4 mm. to 2.0 cm. tall; ramuli in distichous or verticillate arrangement, simple or branched, obtuse, and reduced or lacking toward base of frond...1. *C. ambigua*
    6. Plant 2.5 to 4 cm. tall; ramuli strictly distichously arranged, simple throughout, obtuse to acuminate, continuous to base of frond......3. *C. sertularioides*

1. *C. ambigua* Okam.

C. ambigua Okamura 1897, p. 4, pl. 1, fig. 3–12.

C. Vickersiae Børgesen 1911, p. 129, fig. 2.

Plant minute, 4 mm. to 2.0 cm. tall, filiform; fronds erect, branched, supporting simple to quadridichotomous, cylindrical, verticillately, or distichously arranged ramuli; habit feathery to dense.

Caulerpa ambigua (pl. 22; fig. 2, *a, b*) is very minute and easily overlooked in the field. The majority of specimens were secured with the aid of hand lens and forceps from the protected surfaces of pieces of coral and rocks brought into the laboratory. Some were obtained from the sides of shallow pools. In the process of collecting, the delicate rhizomes were broken and the specimens are fragmentary. For this reason it is impossible to determine the exact nature of the entire plants. The several specimens collected show a diversity in form. A few fronds display a completely distichous arrangement of unbranched ramuli (pl. 22, *a*). In a second type of distichous frond, the ramuli are practically all dichotomous (pl. 22, *b, c*). Intermediate stages between these two were found. Other specimens possess verticillately arranged ramuli which branch profusely (pl. 22, *d–f*). Most plants show zonations which are believed to be the limits of periodic growth. *C. ambigua* is cited here for the first time from the Hawaiian Islands.

Some difficulty was encountered in the identification of *C. ambigua* owing to the belief of certain writers that the species embraces two distinct entities: *C. ambigua* Okam. and *C. Vickersiae* Børgs. A brief review of the history of the two may be of interest. In 1897 Okamura described a plant under the name *C. ambigua*, which he characterized as lacking a prostrate rhizome and possessing articulated rachises and ramuli. In the same paper he also pointed to the similarity between *C. ambigua* and *C. Okamurai* Weber-van Bosse (in Okamura, 1897), which has constricted (or at least pedicellate) ramuli. The articulations he thought of such significance that he placed his plants in the section Sedoideae of the genus, which includes only articulated members. Okamura (1897, pl. 1, fig. 3–12) illustrated *C. ambigua* with a series of ten figures. His figures 4, 6, and 7 show the constricted character, while figures 9 and 10 seemingly represent a plant which lacks articulations and is quite distinct from *C. Okamurai*. None of the ramuli in his figures are branched.

In her monograph of *Caulerpa* in 1898 (p. 388) Weber-van Bosse used the phrase "indistinctement articulé" in discussing *C. ambigua*, while in her Siboga paper of 1913 (p. 97), she pointed out that her *C. ambigua* material was more closely related to *C. elongata*, a member of the section Bryoideae, than to members of the section Sedoideae.

Vickers (1908, pl. 37, fig. 3–6), illustrated *C. ambigua* from Barbados as being distinctly nonconstricted, that is, similar to the nonarticulated plants of Okamura (1897, pl. 1, fig. 9, 10), but in no way resembling his constricted specimens (*op. cit.*, pl. 1, fig. 4, 6, 7).

Børgesen (1911, p. 129, fig. 2), in reporting his West Indian material, was led to the conclusion that Okamura had referred two species to *C. ambigua*, since his West Indian specimens agreed well with the figures of Vickers and with those of the nonarticulated plants of Okamura (1897, pl. 1, fig. 9, 10), but were unlike the latter's articulated specimens. Børgesen, therefore, proposed the name *C. Vickersiae* (originally *C. Vickersii*) for the plants without constrictions.

Taylor in 1928 (p. 104) accepted the specific name *C. Vickersiae* of Børgesen, and added a new variety, *C. Vickersiae* var. *luxurians*. In a later paper (1933, p. 396) he described a second variety, *C. Vickersiae* var. *furcifolia*, of the same species.

Okamura (1931, p. 101), in answering Børgesen's argument, says "... that in my plant two species are not confused may be seen from my Icones [1915] Pl. 139, figure 6, which is a portion of figure 3. In that figure, there may be some irregularities in the arrangement of ramenta having somewhat alternate manner, instead of regularly distichous, and moreover, some of ramenta have constricted base. Figure 5 may be taken as an extreme one of such a frond. Considering on the one hand, that *Caulerpa* is a plant taking several different forms in one and the same species, and on the other, that figure 3 which has not well-defined surculus is not different from figure 1 and 2, I think that my determination is justified."

In Yamada's report of the algae from the Ryukyu Islands (1934, p. 64) *C. Vickersiae* Børgs. is given as a synonym of *C. ambigua* without comment. Among his algae he found four specimens which he referred to *C. ambigua,* three of which were representative of the figure and the description of *C. Vickersiae* as given by Børgesen (1911, p. 129, fig. 2), while in a fourth specimen the ramuli are multiseriately arranged in a dense and irregular fashion.

The Hawaiian material was found to be unquestionably related to Okamura's Japanese plants as well as to Børgesen's *C. Vickersiae.* The diversity of form (pl. 22, and intermediate stages) approximates the range of conditions indicated by Okamura.

I have had occasion to examine some of Okamura's material of *C. ambigua* from Japan (Herb. Univ. Calif. 688774 from Nemoto [Bōshū] distributed as No. 95 in his Exsiccatae of Japanese Algae). All the characters illustrated in his original account of the species (1897, fig. 3–12) are well represented in the above collection. Several additional specimens furnish convincing connecting links between the misunderstood oriental plants and those from the other parts of the world discussed in the foregoing historical account. On the basis of these observations, which have been supplemented by examination of the Hawaiian plants, I conclude that but one species is involved, the proper designation of which is *C. ambigua,* and that *C. Vickersiae* should be considered a synonym of it. Such polymorphism within a species is not unusual for this genus. Okamura probably overstressed the importance of what appeared to be "spurius articulations" in a specimen which he later referred to (1931) as showing an extreme rather than a typical development.

In the material from Hawaii very slight constrictions were occasionally observed at the bases of some of the ramuli. No significance is assigned to them, however, as they are not a typical feature of the plants, and are very obscure at best, showing no regularity of occurrence. Weber-van Bosse's (1898, p. 388) statement "indistinctement articulé" is open to the interpretation that there may have been very slight, although indistinct, constrictions in her plants. Furthermore, Taylor includes as a part of his original description of *C. Vickersiae* var. *furcifolia* (1933, p. 397): "very slightly contracted toward ramular bases." These admissions leave little basis for a split of Okamura's original *C. ambigua* into two species.

Before the absence of a prostrate rhizome can be relied upon as a distinguishing feature of *C. ambigua,* it must be remembered that in such a delicate and minute plant, the chance of destroying the rhizome in collecting is great. The specimens of Okamura and of Dodge, Dodge, and Thomas (Herb. Univ. Calif 688774 and 437251 respectively) have rhizomes which are partly prostrate.

The practice of supplying varietal designations to closely related plants within a species has been common in the genus *Caulerpa,* and is adhered to here, although these varieties are, for the most part, not clearly definable, being connected by transitional forms.

Type locality: Ogasawarajima (Bonin Islands).

Geographic distribution: Ogasawarajima (Bonin Islands); Nemoto (Bōshū); Ryukyu Islands; Kôtôsho (Botel Tobago); Virgin Islands; Barbados; Florida; Puerto Limon, Costa Rica; Oahu, Hawaiian Islands.

KEY TO HAWAIIAN VARIETIES

1. Fronds beset with simple to twice-dichotomous, distichously arranged ramuli; plant usually loose and feathery.. ......(2)
1. Fronds beset with densely furcate, multiseriately arranged ramuli; plant often heavily imbricate..*d.* var. *furcifolia*
    2. Short simple ramuli alternating with longer dichotomously branched ramuli on a single frond........................ ....*a.* var. *Vickersiae*
    2. Ramuli usually unbranched throughout...........................*b.* var. *simplex*
    2. Ramuli usually once to twice-dichotomously branched throughout....*c.* var. *dichotoma*

1*a.* *C. ambigua* var. **Vickersiae** (Børgs.) comb. nov.

C. Vickersii (corrected to *C. Vickersiae*) Børgesen 1911, p. 129, fig. 2.

Fronds beset with zones of distichously arranged ramuli; short unbranched ramuli alternating with longer dichotomous ramuli.

Members of this variety are considered to be intermediate between *C. ambigua* var. *simplex* and *C. ambigua* var. *dichotoma* (cf. pl. 22, *a–c*). The figures of Børgesen (1911, p. 129, fig. 2, as *C. Vickersiae*) and of Yamada (1934, p. 64, fig. 33, as *C. ambigua*) are illustrative of this variety.

Børgesen (1913, p. 121), in discussing the characteristic periodic zonation in *C. ambigua,* implied that the shorter unbranched ramuli toward the apical region of each zone were less vigorous stages, and that the basal ramuli of each zone represented a more developed condition in which they became noticeably longer and dichotomized.

Collection: Papenfuss 10508, Feb. 15, 1942, Waikiki, reef in front of the Halekulani Hotel, Oahu.

Type locality: Virgin Islands.

Geographic distribution: Virgin Islands; Ryukyu Islands; Oahu, Hawaiian Islands.

1*b.* *C. ambigua* var. **simplex** var. nov.

C. ambigua var. **simplex** var. nov.

Planta disticha, frondes cum ramulis simplicibus.

Frond beset with distichously arranged unbranched ramuli, dichotomous ramuli rare to completely lacking.

Plate 22, *a,* illustrates the nature of the terete, filiform, unbranched ramuli which characterize *C. ambigua* var. *simplex.* Several of the plants of Okamura from Nemoto (Herb. Univ. Calif. 688774) and the material of Dodge, Dodge, and Thomas from Costa Rica (Herb. Univ. Calif. 437251) fit well into this category. The plants illustrated by Okamura in 1897 (figs. 7–10) are also representative of this variety. *Caulerpa ambigua* var. *simplex* might be considered to be in keeping with Taylor's *C. Vickersiae* var. *luxurians*[1] but as its members are not necessarily luxuriant in form, as is true of Okamura's plants from Nemoto, it seems best at present to regard them as separate entities.

That *C. ambigua* var. *simplex* is distinct from *C. ambigua* var. *Vickersiae* becomes more convincing in the light of the interpretation of Børgesen (with reference to *C. Vickersiae*) concerning the difference in form of the ramuli of a given frond. He suggested that the first-formed ramuli of each growth period of *C. Vickersiae* tend to be longer and to dichotomize. The striking feature of *C. ambigua* var. *simplex* is that the first-formed ramuli maintain an unbranched condition almost without exception.

Collections: Papenfuss 10507*a*, *type*, and 10507*b*–*f*, Feb. 15, 1942, Waikiki reef in front of the Halekulani Hotel, Oahu; Okamura (Herb. Univ. Calif. 688774), Nemoto; Dodge, Dodge, and Thomas (Herb. Univ. Calif. 437251), Costa Rica.

Type locality: Waikiki, Oahu, Hawaiian Islands.

Geographic distribution: Ogasawarajima (Bonin Islands); Nemoto (Bōshū); Costa Rica; Oahu, Hawaiian Islands.

1*c*. *C. ambigua* var. **dichotoma** var. nov.

C. ambigua var. **dichotoma** var. nov.

Planta disticha, frondes cum ramulis dichotomis.

Fronds beset with distichously arranged ramuli, which are usually once to twice dichotomous.

Variety *dichotoma* is proposed for certain Hawaiian plants (pl. 22, *b*, *c*) in which the ramuli throughout the frond are dichotomously forked. If the morphology of the ramuli is indicative of genetic variation in *C. ambigua*, as seems possible among varieties in certain other species of this genus, the simple or forked character of the ramuli of the varieties of *C. ambigua* would then serve to distinguish *C. ambigua* var. *dichotoma* from both *C. ambigua* var. *simplex* and *C. ambigua* var. *Vickersiae*.

Collections: Eubank 627, *type*, and 628, May 2, 1942, Marine Biological Laboratory at Waikiki, Oahu.

Type locality: Waikiki, Oahu, Hawaiian Islands.

Geographic distribution: Oahu, Hawaiian Islands.

1*d*. *C. ambigua* var. **furcifolia** (Taylor) comb. nov.

C. Vickersiae var. *furcifolia* Taylor, 1933, p. 396.

Fronds beset with densely furcate, multiseriately arranged ramuli; plant usually heavily imbricate.

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[1] A new combination of *C. Vickersiae* var. *luxurians* is apropos at this time even though no Hawaiian plants have been assigned to it: *C. ambigua* var. **luxurians** (Taylor) comb. nov. Taylor, 1928, p. 104.

The Hawaiian plants of *C. ambigua* var. *furcifolia,* as illustrated in plate 22, *d–f,* are well within the limits of the category as set forth by Taylor. There are obvious local variations in gross structure. Some plants possess distichously arranged simple ramuli at their terminal portions, becoming whorled and densely furcate toward the base of the frond (pl. 22, *e*). Except for the fact that the ramuli are forked, the habit of the plant in plate 22, *e,* is not far removed from Okamura's plants from Ogasawarajima, in which the ramuli are simple (1897, fig. 3, 4, 6). Several of his plants from Nemoto (Herb. Univ. Calif. 688774) actually have furcate ramuli. Other Hawaiian specimens show the multiseriate condition along the entire frond axis, and all ramuli appear to be forked (pl. 22, *f*). Yamada (1934, p. 65) states that the verticillate plants seem to branch much more profusely than the distichous. He gathered a specimen from Ryukyu which presumably fits into variety *furcifolia.* A duplicate of the material of Dodge *et al.* from Costa Rica (Herb. Univ. Calif. 437251) upon which *C. Vickersiae* var. *furcifolia* Taylor is based, completely lacks forked ramuli, thus showing that *C. ambigua* var. *simplex* as well as *C. ambigua* var. *furcifolia* occurs in Costa Rica.

Collections: Eubank 612–625, May 2, 1942, Marine Biological Laboratory at Waikiki; Eubank 626, May 16, 1942, reef at foot of Puu O Hulu, near Nanakuli, Oahu.

Type locality: Costa Rica.

Geographic distribution: Costa Rica; Ryukyu; Nemoto (Bōshū); Oahu, Hawaiian Islands.

2. *C. Webbiana* Mont.

C. Webbiana Montagne 1838, p. 129, pl. 6.

Plant small, .5 to 2 cm. tall; fronds erect, simple or branched, densely beset with whorls of furcate, mucronate ramuli, 4 or 5 per node; prostrate rhizome usually naked.

In Hawaii, *C. Webbiana* (fig. 1, *d–f*; 2, *c*) is not infrequently found on small rocks in shallow water or in tidal pools in coral reefs. Because of its small size it is often overlooked. At first glance it resembles a greatly dwarfed *Codium,* having a dark green spongy appearance. The ramuli of the frond come off in whorls of four typically (occasionally in whorls of five) as shown in figure 1, *e,* and are intricately branched near their apices, with one or two sharply definable hyaline mucrons at the tip of each ramular dichotomy. The only previous record of this plant from Hawaii was given by Neal (1930, p. 46) with the following comment: "Setchell determined this *Caulerpa* as very near to *pickeringii,* at least probably in the same group."

Collections: Papenfuss 10511, March 29, 1942, Halona; Papenfuss 10513 and Eubank 509, April 14, 1942, Waikiki reef, Honolulu; Papenfuss 10512 and Eubank 508, May 16, 1942, reef at foot of Puu O Hulu near Nanakuli; Eubank (leg. Conger) 562, Oct. 24, 1942 and 547, Nov. 1942, Waikiki reef at Marine Biological Laboratory, Honolulu; Herb. Univ. Calif. 622065 (leg. Neal), Oahu, Hawaiian Islands.

Type locality: Canary Islands.

Geographic distribution: Canary Islands; Barbados; Virgin Islands; Florida; Japan; Oahu, Hawaiian Islands.

2a. *C. Webbiana* var. **Pickeringii** (Harvey and Bailey) comb. nov.

C. Pickeringii Harvey and Bailey 1851, p. 373.

Plant 3 mm. to 4 cm. tall; creeping rhizome and erect fronds covered with whorls of furcate ramuli, 6–12 at each node; ramular apices mucronate.

So far as is known, this variety (fig. 1, *a–c*) is restricted to the islands of the South Pacific and does not occur in Hawaii. In the course of examining the herbarium material at the University of California, I came across a specimen from Oahu collected and identified by Neal as *C. Pickeringii* (Herb. Univ. Calif. 622065, referred above to *C. Webbiana*). Its striking resemblance to *C. Webbiana* prompted further study of *C. Pickeringii.* In most respects Montagne's (1838, p. 129) description of *C. Webbiana* and that of Harvey and Bailey of *C. Pickeringii* are similar. Examination of part of the original material of *C. Pickeringii* has shown the plant to differ from *C. Webbiana* in the following features: (1) The rhizome of *C. Pickeringii* is densely pubescent with ramular scales which are morphologically identical to the ramuli of the fronds, whereas the rhizome of *C. Webbiana* is usually glabrous. (2) *C. Pickeringii* is stouter, the rhizome and the fronds ranging from 2 to 2.5 mm. in thickness and the ramuli reaching a length of 1 mm. The Hawaiian material of *C. Webbiana* is noticeably smaller, the rhizome never exceeding 740 microns in thickness and the ramuli averaging about 600–740 microns in length. (3) In *C. Pickeringii* the ramuli occur in whorls of six to twelve (or possibly more) on the frond axis, whereas *C. Webbiana* usually has but 4 ramuli per node (cf. fig. 1, *c, e*).

The name *C. Pickeringii* has been overlooked by a majority of workers, including J. Agardh (1872, pp. 1–44) and De Toni (1889, pp. 441–487). Weber-van Bosse (1898, p. 272) apparently saw part of the Harvey and Bailey material but retained *C. Pickeringii* as an independent species. In a later paper (1910, p. 8) she suggested that *C. Pickeringii* is phylogenetically more advanced than *C. Webbiana,* and placed the two species side by side in the section Bryoideae. In my opinion, however, the differences between *C. Webbiana* and *C. Pickeringii* are not of sufficient magnitude to justify separation into distinct species and it seems best to reduce the latter to a variety of the former. Actually the habit of the two plants, as well as the ramular arrangement and the general morphology, appear to be identical. Even though this plant does not occur in Hawaii, a new combination seems justified at this time.

Collections: Eua, Tonga, Herb. Univ. Calif. 667642; Tahiti, Herb. Univ. Calif. 667634; Fakarava Atoll, Paumota Group, Herb. Univ. Calif. 667635; Wilson Islands, Paumota Group, Herb. Univ. Calif. 677620 (part of the original material of Harvey and Bailey of *C. Pickeringii*).

Type locality: Wilson Islands, Paumota Group.

Geographic distribution: South Pacific Islands including: Tonga; Tahiti; Wilson Islands and Fakarava Atoll, Paumota Group.

3. *C. sertularioides* (Gmel.) Howe

C. sertularioides (Gmel.) Howe 1905, p. 576.

Plant 2.5 to 4 cm. tall, yellow-green, feathery; frond axis cylindrical, erect; ramuli distichous, opposite, terete, simple, obtuse to acuminate.

This is a beautiful and delicate plant (fig. 2, *d, e*) found in warm quiet waters of tidal pools or creeping along the sandy sea floor. The species is recorded here for the first time from the Hawaiian Islands.

Collections: Papenfuss 10514, Sept. 3, 1940; Papenfuss 10518, Dec. 15, 1940; Papenfuss 10515, Mar. 30, 1941; Papenfuss 10517, Dec. 15, 1941; Papenfuss 10516 (leg. Conger); Eubank 511, Jan. 12, 1942; Eubank 514, Mar. 1, 1942—all from Hanauma Bay. Eubank 512, Nov. 2, 1941, near Makapuu Point, Oahu.

Type locality: Gmelin (1768) gave no definite locality other than "in corallis americanis."

Geographic distribution: In all tropical seas.

4. *C. taxifolia* (Vahl) Ag.

C. taxifolia (Vahl) Agardh 1822, p. 435.

Plant 3 to 10 cm. tall; frond axis erect, laterally compressed; ramuli about 4 mm. long, distichous, opposite, laterally compressed, simple, usually tending to be sickle-shaped, apices mucronate.

In Hawaii, *C. taxifolia* (fig. 2, *f, g*) is locally abundant in quiet water or in tidal pools. A comparison of the descriptions and of specimens of *C. taxifolia* and *C. crassifolia* (Ag.) J. Agardh (1872, p. 13) suggests that the two may be cospecific. In *C. crassifolia* the thallus seems to be of larger stature and the pinnae flatter and broader, but these are features of minor importance. The name *C. taxifolia* is retained for the Hawaiian plants since the material conforms to the descriptions of this species and since, in any event, this name antedates *C. crassifolia.*

C. taxifolia was first reported from Hawaii by Chamberlain (1880), later by Tilden (1901) and MacCaughey (1918). Chamberlain also listed *C. asplenioides* Grev., which name, according to De Toni (1889, p. 452), is synonymous with *C. taxifolia.* Through the kindness of Dr. David H. Linder, I have had the opportunity of examining the Chamberlain material of *C. asplenioides* and *C. taxifolia* in Herbarium Farlow. The specimens of both were found to be of the latter species. The determination of Tilden's specimen of *C. taxifolia* in her *Exsiccatae of American Algae* (1901, Century V, No. 452) has been verified also.

Lemmermann (1905), and later MacCaughey (1918), who took the record from Lemmermann, report *C. pinnata* (L.) Weber-van Bosse from Laysan on the northern extremity of the Hawaiian Archipelago. Since this name was employed by Weber-van Bosse for the plant currently known as *C. crassifolia,* an entity which, to my knowledge, has not been found in Hawaii, and since the latter resembles *C. taxifolia,* a quite common species from Hawaiian shores, it seems probable that the record in question applies to *C. taxifolia.*

Collections: Papenfuss 10520, Oct. 4, 1941, Puuloa Beach (leg. Kawahara), deep-water form; Papenfuss 10523, Nov. 2, 1941, near Makapuu Point; Papenfuss 10519, Nov. 23, 1941, Nanakuli reef; Papenfuss 10521 and Eubank 510, May 16, 1942, reef at foot of Puu O Hulu near Nanakuli, Oahu.

Type locality: St. Croix, Virgin Islands.

Geographic distribution: Virgin Islands; Barbados; Ceylon; Oahu, Hawaiian Islands.

5. *C. serrulata* var. *typica* (Weber-van Bosse) Tseng.

C. serrulata (Forsskål) J. Agardh emend. Børgs. var. *typica* (Weber-van Bosse) Tseng. Børgesen 1932, p. 5; Tseng 1936, p. 178, pl. 1.

Plant 1 to 4 cm. tall; fronds laterally compressed with mucronate serrations along the margins, sessile, usually twisted, asymmetrical, lacking ramuli but often with proliferations; texture membranaceous.

The nature of the marginal serrations of the frond, the frequent presence of twisted laminae, and the absence of pedicels distinguish variety *typica* from the other varieties of *C. serrulata*. The following three forms of this variety are represented in the material seen from Hawaii (fig. 2, *h–j*).

Howe (1934) reported *C. serrulata* from the Pearl and Hermes Reef which is at the northwesternmost tip of the Hawaiian chain.

Type locality: Red Sea.

Geographic distribution: Red Sea; Ceylon; Mariana Islands; Hainan; Ryukyu Islands; Formosa; Tonga; Philippine Islands; Oahu and Pearl and Hermes Reef, Hawaiian Islands.

5a. *C. serrulata* var. *typica* f. *lata* (Weber-van Bosse) Tseng.

C. serrulata var. *typica* f. *lata* (Weber-van Bosse) Tseng. 1936, p. 178, pl. 1.

Twisted fronds with distinct mucronate serrations along infolded margins.

Collections: Papenfuss 10524, Aug. 21, 1941; 10525, May 2, 1942, Waikiki reef at Marine Biological Laboratory, Honolulu. Papenfuss 10522, Dec. 15, 1940; 10510, Sept. 30, 1940; Papenfuss and Eubank (leg. Conger) 516, Sept. 20, 1942,—all from Hanauma Bay, Oahu. Herb. Univ. Calif. 622028 (leg. Rock), Oahu, Hawaiian Islands.

5b. *C. serrulata* var. *typica* f. angusta (Weber-van Bosse) comb. nov.

C. Freycinetii var. *typica* f. *angusta* Weber-van Bosse 1898, p. 313, pl. 25, fig. 4*b*.

Twisted fronds with distinct mucronate serrations along free margins, lacking serrations along infolded parts.

Collections: Papenfuss 10526, April 11, 1941, foot of Koko Head; Papenfuss 10574, Nov. 30, 1941, Black Point, Oahu; Herb. Univ. Calif. 622027 (leg. Reed), Hawaiian Islands.

5c. *C. serrulata* var. *typica* f. *serrulata* (Weber-van Bosse) Gilbert

C. serrulata var. *typica* f. *serrulata* (Weber-van Bosse) Gilbert 1942, p. 15.

Fronds scarcely twisted, if at all; marginal serrations regular throughout frond.

Collections: Papenfuss 10541, Mar. 1, 1942, Hanauma Bay; Eubank (leg. Conger) 545, Nov. 1942, Waikiki reef at Marine Biological Laboratory; Eubank 562, October 11, 1942, Marine Biological Laboratory, Waikiki, Oahu, Hawaiian Islands.

6. *C. lentillifera* J. Ag.

C. lentillifera J. Agardh 1837, p. 173.

Plant 1 to 3 cm. tall; fronds erect, cylindrical, with pedicellate, unbranched, globose ramuli, which are inserted verticillately; ramuli about 2 mm. long, constricted at point of attachment of pedicel to terminal head.

The fronds of *C. lentillifera* (fig. 2, *k, l*) resemble bunches of grapes. The constricted character of the ramuli is a constant feature of the species, and is the only character distinguishing this species from members of the *C. racemosa* group. It is conceivable that it is only a variety of *C. racemosa*. This is the first record of the occurrence of *C. lentillifera* in Hawaii.

Collection: Eubank 528, Jan. 12, 1942, Hanauma Bay, Oahu.
Type locality: Red Sea.
Geographic distribution: Red Sea; Madagascar; Ceylon; Oahu, Hawaiian Islands.

7. *C. racemosa* (Forsskål) J. Ag.

C. racemosa (Forsskål) J. Agardh 1872, p. 35.

Plant 2 mm. to 4 cm. tall; fronds beset with pedicellate ramuli, which may be globose, obovate, plano-convex, or discoid; ramuli at times occurring singly on the rhizome.

C. racemosa (fig. 2, *m–w*) is a composite of overlapping varietal types which differ from one another only in degree. Members of this species are common in tidal pools in the littoral zone, on reefs, or in quiet waters of the upper sublittoral belt. But two varieties of *C. racemosa* have been reported from the Hawaiian Islands. Lemmermann (1905), and later MacCaughey (1918) accredit *C. racemosa* var. *laetevirens* to Laysan. I have seen no specimen which can definitely be referred to var. *laetevirens*. *C. clavifera*, now known as *C. racemosa* var. *clavifera*, was reported from Oahu by Chamberlain (1880) but was not secured by me, nor were Hawaiian representatives of this variety found in the various other collections examined.

Geographic distribution: Throughout all tropical seas.

KEY TO HAWAIIAN VARIETIES

1. Ramular apex a flattened or cup-shaped disc, peltately attached to pedicel........... (2)
1. Ramular apex clavate, pyriform, globose or plano-convex, usually pedicellate........ (3)
    2. Ramular disc with smooth margin; plant 1–3 cm. tall.................. *7d.* var. *peltata*
    2. Ramular disc scalloped or dentate at margin; plant 2 mm. to 1 cm. tall.. *7e.* var. *exigua*
3. Ramuli often occurring singly on rhizome, apex spherical........................ (4)
3. Ramuli on distinct assimilative fronds, apex pyriform to plano-convex.............. (5)
    4. Plant minute, rarely taller than 6 mm.; ramular apex about 1–2 mm. in diameter .... *7a.* var. *microphysa*
    4. Plant stouter, 2 cm. or more tall; ramular apex 4–6 mm. in diameter .... *7b.* var. *macrophysa*
5. Frond 5 mm. to 1 cm. tall; plant densely imbricate; ramular apex minute, 1 to 1.5 mm. in diameter, ranging on a single frond from pyriform to plano-convex in shape .... *7f.* var. *imbricata*
5. Frond 1.5 to 3 cm. tall; ramular apex rather constantly plano-convex in shape, 1.5–2 mm. diameter... *7c.* var. *turbinata*

7a. C. racemosa var. *microphysa* (Weber-van Bosse) Taylor

C. racemosa var. *microphysa* (Weber-van Bosse) Taylor 1928, p. 102, pl. 12, fig. 14; pl. 13, fig. 11.

Fronds 4 to 6 mm. high, thinly scattered on the stolon, branched or simple, giving rise to a loose arrangement of spherical, pedicellate ramuli, the latter often occurring singly on rhizome; ramular apex 1 to 2 mm. in diameter.

This variety (fig. 2, *m*) has not previously been reported from Hawaii.

Collection: Eubank 529, May 16, 1942, reef at foot of Puu O Hulu, Oahu.
Type locality: Macassar.
Geographical distribution: All tropical seas.

7b. *C. racemosa* var. *macrophysa* (Kütz.) Taylor

C. racemosa var. *macrophysa* (Kütz.) Taylor 1928, p. 101, pl. 12, fig. 3; pl. 13, fig. 9.

Fronds 2 or more cm. high, thinly scattered on the stolon, giving rise to a loose arrangement of spherical, pedicellate ramuli, the latter often occurring singly on the rhizome; ramular apices 4–6 mm. in diameter.

Caulerpa racemosa var. *macrophysa* (fig. 2, *n*) is reported here for the first time from the Hawaiian Islands. When Kützing (1857, p. 6) created the specific name *Chauvinia macrophysa* he described the ramuli as "inflatis obovatis subglobosis." Weber-van Bosse (1898, p. 361), who reduced the entity to a form of *Caulerpa racemosa* var. *clavifera,* characterized the ramuli as globose and 4 to 5 mm. in diameter. She also introduced a new form, *C. racemosa* var. *clavifera* f. *microphysa,* which is similar to *C. racemosa* var. *clavifera* f. *macrophysa* but with the globose ramuli measuring at most only 1 mm. in diameter. Taylor (1928, p. 101) records both forms from Florida, but elevates them to varietal rank under *C. racemosa.* However, his description of *C. racemosa* var. *macrophysa* is not in agreement with that of Kützing, for he describes the ramuli as convex or nearly so, distinguishing it from *C. racemosa* var. *microphysa,* in which the ramuli are spherical. Setchell apparently noticed this discrepency for he made a marginal note in his copy of Taylor's work to the effect that Taylor's plant was not based on the criteria employed by Kützing. In accord with Taylor, I regard these entities as varieties of *C. racemosa,* although it may be noted that the Hawaiian representatives of both varieties possess globose to subglobose ramular apices.

Collections: Papenfuss 10527, Sept. 3, 1940; Papenfuss 10528, Dec. 15, 1940, both from Hanauma Bay, Oahu.
Type locality: Coast of Central America.
Geographic distribution: All tropical seas.

7c. *C. racemosa* var. **turbinata** (J. Ag.) comb. nov.

C. clavifera var. *turbinata* J. Agardh 1837, p. 173.
C. racemosa var. *Chemnitzia* Weber-van Bosse 1898, p. 370.

Fronds 1.5–4 cm. high, erect, densely beset with plano-convex, trumpet-shaped ramuli approximately 2 mm. in length.

This variety (fig. 2, *o–q*) is very common in Hawaii, occurring at practically every locality visited. Close examination shows a diversity of ramular shapes to exist on a single plant or even upon a single frond. Figure 2, *t,* illustrates a common condition in which the diversity within a single plant is so great that the specimen can not be placed in any single taxonomic category. Clavate, "uviferoid," "laeteviroid," and peltate ramuli are all present. In some less extreme specimens, for the sake of convenience, classification is based upon the ramular type which is most prevalent on a given plant. Occasionally, proliferating ramuli were found (fig. 2, *q*) in which an outgrowth had developed from the apical margin and had become extended into another ramulus, which in turn produced proliferations.

For almost half a century *C. racemosa* var. *turbinata* (J. Ag.) has been known as *C. racemosa* var. *Chemnitzia* (Esper) Weber-van Bosse. Weber-van Bosse (1898, p. 370), in making the varietal combination from *Fucus Chemnitzia* Esper (1798), included as a synonym the *C. clavifera* var. *turbinata* of J. Agardh (1837); and from J. Agardh's description it is clear that *C. racemosa* var. *turbinata* actually is synonymous with *C. racemosa* var. *Chemnitzia.* According to Article 58 of the International Rules of Botanical Nomenclature (1935) the former has priority.

C. racemosa var. *turbinata* was reported from Hawaii by Chamberlain (1880) as *C. Chemnitzia.*

Collections: Papenfuss 10530, Sept. 3, 1940; Papenfuss 10529, Dec. 15, 1941; Papenfuss 10531, Jan. 12, 1942 (leg. Conger); Eubank 530, Mar. 1, 1942—all from Hanauma Bay. Papenfuss 10543, Nov. 23, 1941, Nanakuli; Papenfuss 10540, May 2, 1942, Waikiki reef in front of Marine Biological Laboratory, Honolulu; Eubank 560, May 31, 1942, Kahala reef; Herb. Univ. Calif. 622057 (leg. Reed), Koloa Point, Oahu.

Type locality: Red Sea.

Geographic distribution: All tropical seas.

7*d*. *C. racemosa* var. **peltata** (Lamx.) comb. nov.

C. peltata Lamouroux 1809, p. 145.

Plant 1 to 3 cm. high; fronds producing pedicellate, peltate ramuli with cup-shaped or flattened apical discs, 3 to 5 mm. in diameter; margins without serrations, frequent proliferations originating either from center or from margin of apical disc.

The Hawaiian material (fig. 2, *r*, *s*) presents convincing evidence that *C. peltata* is not a distinct species and should be reduced to a variety of *C. racemosa.* Numerous collections, such as that illustrated in figure 2, *t*, demonstrate transitional stages which often occur on a single plant. Even plants which at first glance appeared to be entirely peltate, proved upon examination to possess various erratic ramuli which were identical with the characteristic trumpet-shaped ramuli of *C. racemosa* var. *turbinata* or the clavate structure of *C. racemosa* var. *clavifera.* The removal of *C. peltata* to varietal rank under *C. racemosa* is further supported by the following suggestions of early and modern workers in the field:

Lamouroux (1809, p. 145) commented: "Cette espèce se rapproche singulièrement de la précédente [*C. Chemnitzia*]." He made reference to the diversity of ramular types found on a single plant, but attributed it to desiccation and suggested that it would not be found in living plants.

Zanardini (1858, p. 287) concluded that *C. peltata* Lamx. should be a variety of *C. Chemnitzia* because of its striking resemblance to it.

Weber-van Bosse (1898, p. 374) discussed the problem somewhat more fully: "Le *C. peltata* Lamx. a été considéré par Turner, Decaisne et Zanardini, comme une variété du *C. Chemnitzia,* et Harvey l'a déterminé pour *C. clavifera* var. *platydisca* [nomen nudum]. J'ai tâché de démontrer qu'il est plus logique de regarder le *C. Chemnitzia* comme une variété intermédiaire entre le *C. racemosa* et le *C. peltata;* ce dernier, vu les nombreux cas où la forme des ramules est constante, et les variétés qu'il fait naître, peut être considéré comme sous-espèce distincte. Je dis sous-espèce, car on rencontre de nouveau trop souvent des échantillons à ramules peltés et an massue, pour qu'on puisse fermer les yeux à l'étroit lien de parenté qui unit le *C. peltata* ou *C. racemosa.*"

Børgesen (1925, pp. 113–115, fig. 48, *a–c*) included the following remarks in his discussion of *C. peltata:* "The shape of the thallus is highly variable.... In other specimens the shape of the branchlets was not so markedly peltate (cf. fig. 48, *a, b*). The upper surface of the branchlets in these plants was not flat but often somewhat convex and the stipe was broadly conical making a rather even transition to the disc.... All the tufts I have seen had branchlets of more or less varying shape making even transitions from those of *Caulerpa racemosa* to var. *Chemnitzia* and further to *Caulerpa peltata.* Pure tufts were found only of the latter form, for which reason I refer the different forms found to this 'species' [*C. peltata*]."

Gilbert (1942, p. 22), basing his observations on material from the Philippine Islands and Java, remarked: "In this species [*C. peltata*] have been included all those specimens with few to all peltate ramuli. Transition forms are found in the specimens listed under var. *typica;* they vary from plants in which all ramuli are peltate to ones in which only a few of the ramuli are typically peltate and the others range in shape to the clavate form of *Caulerpa racemosa* var. *clavifera,* the trumpet-like and imbricate ramuli of *C. racemosa* var. *Chemnitzia,* or the suddenly expanded spherical-tipped ramuli of *C. racemosa* var. *occidentalis.* All these transition forms may at times be found on the same plant and largely even on the same frond. This serves to illustrate once again that the line distinguishing *C. peltata* from *C. racemosa* is apparently quite arbitrary."

No previous record has been made of this variety from the Hawaiian Group.

Collections: Papenfuss 10532, Sept. 3, 1940; Papenfuss 10533, Mar. 1, 1942, and Eubank 540 (leg. Conger), Sept. 20, 1942—all from Hanauma Bay. Eubank 519, Nov. 23, 1941, Nanakuli; Eubank 523, Nov. 30, 1941, Black Point; Eubank 527, May 16, 1942, reef at foot of Puu O Hulu; Eubank 518, Mar. 27, 1942, between Blow Hole and Makapuu Point, Oahu.

Those collections which are not classifiable owing to the diversity of ramular types are: Papenfuss 10534 and Eubank 524, Nov. 30, 1941, Black Point; Eubank 521, Mar. 1, 1942, Hanauma Bay; Papenfuss 10535 and Eubank 525, April 19, 1942, Halona Reef, Oahu.

Type locality: Antilles.

Geographic distribution: All tropical seas.

7e. *C. racemosa* var. **exigua** (Weber-van Bosse) comb. nov.

C. peltata var. *exigua* Weber-van Bosse 1898, p. 377.

Plant small, 2 to 4 mm. to occasionally 1 cm. in height; rhizome usually producing single ramuli, occasionally fronds; flattened peltate ramular discs 1 to 3 mm. in diameter with irregular serrations and proliferations at the margins.

This is the first record of *C. racemosa* var. *exigua* (fig. 2, *u, v*) from Hawaii. The plants of this variety appear to be more constant in their form than *C.*

racemosa var. *peltata*. *C. racemosa* var. *exigua* is considered to be of equal rank with the preceding members of the *C. racemosa* complex because the serrations of the apical margins of the ramuli delimit these plants as sharply as the various shapes and sizes of the ramuli of other varieties of *C. racemosa*.

Collections: Papenfuss 10536, Mar. 29, 1942; Papenfuss 10537, April 19, 1942, Halona Reef; Papenfuss 10538 and Eubank 533, May 16, 1942, reef at foot of Puu O Hulu near Nanakuli, Oahu.

Type locality: Not indicated by Weber-van Bosse (1898, p. 377).

Geographic distribution: Samoa; Mangaia; Oahu, Hawaiian Islands.

7f. *C. racemosa* var. **imbricata** (Kjellm.) comb. nov.

Chauvinia imbricata Kjellman, in Wittrock and Nordstedt, Exsiccatae, No. 436.

Caulerpa peltata var. *typica* f. *imbricata* Weber-van Bosse 1898, p. 375.

Plant small, .5 to 1 cm. tall, densely imbricate; ramuli rarely over 1 to 1.5 mm. in diameter, with inflated apices which vary from plano-convex to obovate.

Weber-van Bosse (1898, p. 375) placed *C. racemosa* var. *imbricata* as a form of *C. peltata*, while Svedelius (1906, p. 134) retained its specific rank. Svedelius's figures 37, 38, and 40 to 42, which are based on Ceylon plants, resemble the habit of the Hawaiian plants. Because the ramular types of the plants in question are strictly within the limits of the *C. racemosa* group, a separate species designation is superfluous. *C. racemosa* var. *imbricata* is considered here to be based on the small and densely imbricate nature of the ramuli (fig. 2, *w*), which may range in shape from obovoid to peltate on a given plant. However, in assigning varietal rank, I admit doubt about its correct status. Its rather constant growth form seems to justify consideration of it as an autonomous entity. On the other hand, it may be but an ecological variant of any one of several varieties of *C. racemosa*. No previous record of this variety has been made from Hawaii.

Collections: Eubank 532, Jan. 12, 1942; Eubank 559, Mar. 1, 1942, Hanauma Bay; Eubank 531, Mar. 27, 1942, between Blow Hole and Makapuu Point; Eubank 561, April 19, 1942, Halona Reef; Papenfuss 10542, April 1, 1942, Waikiki Reef at Elks Club, Honolulu; Papenfuss 10539, May 2, 1942, Waikiki reef in front of Marine Biological Laboratory; Eubank 520, May 16, 1942, reef at foot of Puu O Hulu, Oahu; Herb. Univ. Calif. 622066 (leg. Reed) foot of Diamond Head, Oahu, Hawaiian Islands.

Type locality: Ceylon.

Geographic distribution: All tropical seas.

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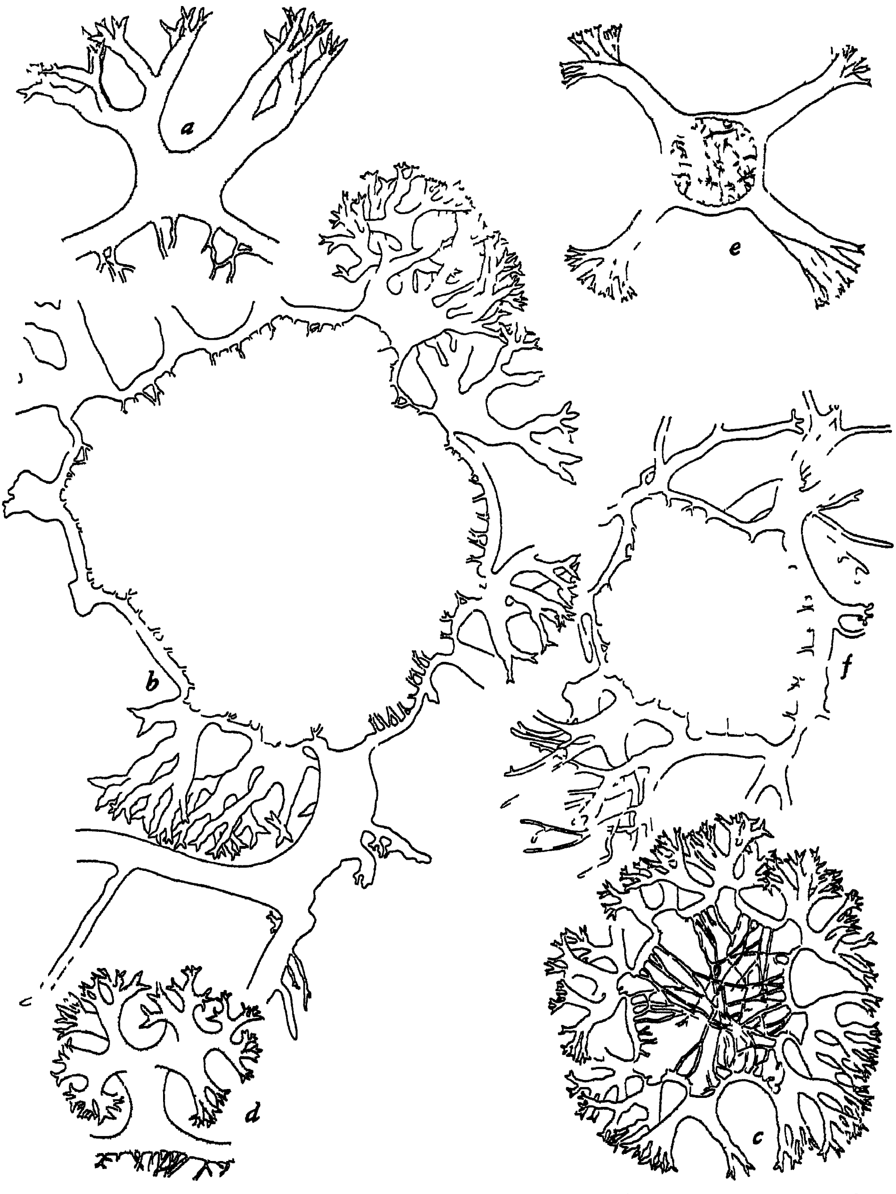


Figure 1. *Caulerpa Webbiana* (camera lucida drawings): (*a*) Var. *Pickeringii* (from Harvey and Bailey collection from the Wilson Islands). Ramulus of frond showing mode of branching and mucronate apices. × 37. (*b*) Var. *Pickeringii* (from Harvey and Bailey collection from the Wilson Islands). Transverse section of rhizome showing rhizoids and whorl of ramuli. × 32. (*c*) Var. *Pickeringii* (from Harvey and Bailey collection from the Wilson Islands). Transverse section of frond, showing trabeculae and whorl of 8 ramuli. × 16. (*d*) (Hawaiian plant). Ramulus of frond showing mode of branching and mucronate apices. × 32. (*e*) (Hawaiian plant). Transverse section of frond showing trabeculae and whorl of 4 ramuli. × 23. (*f*) (Hawaiian plant). Transverse section of rhizome showing rhizoids. Ramuli lacking. × 28.

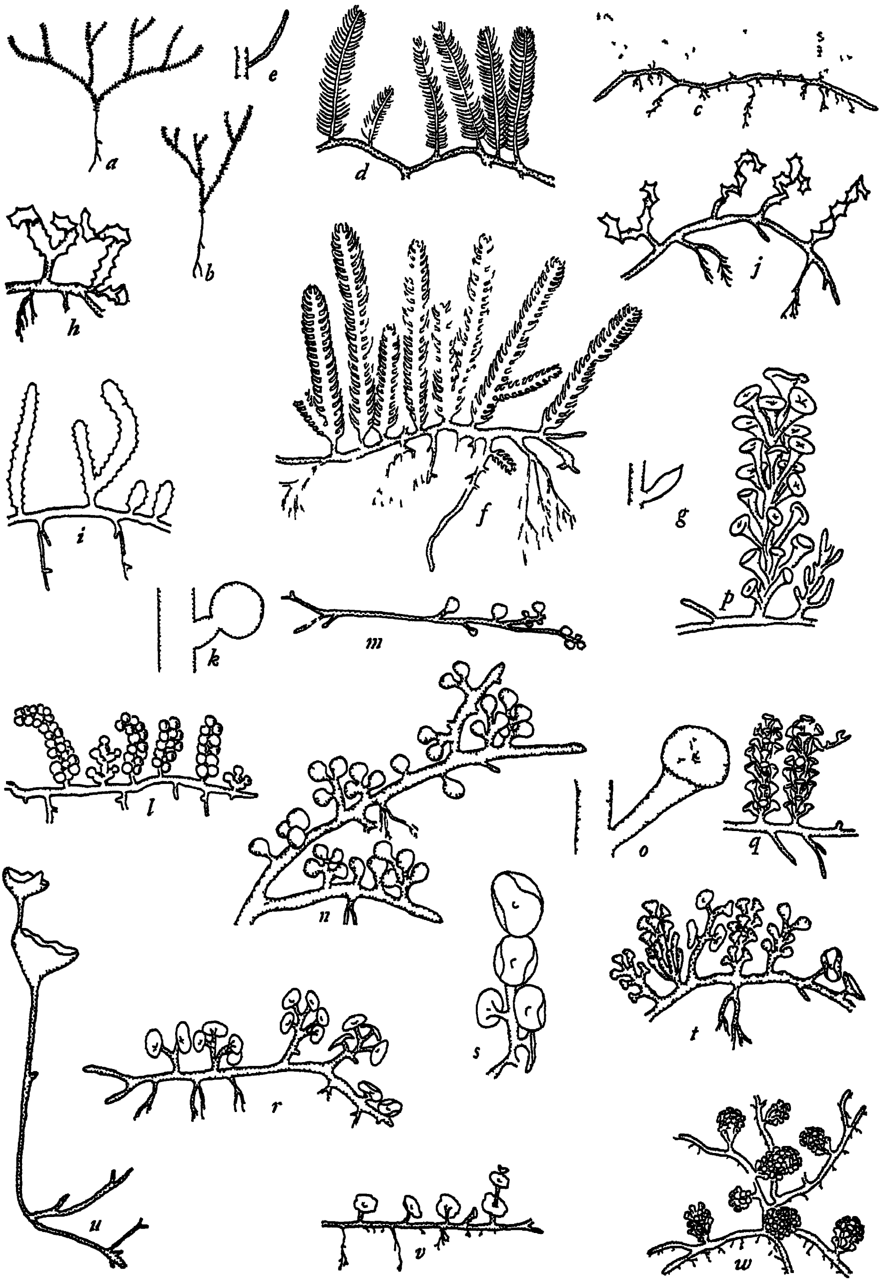


Figure 2. Freehand sketches of all known Hawaiian representatives of the genus Caulerpa: (*a*) *C. ambigua*, habit of distichous plant. × 4. (*b*) *C. ambigua*, habit of verticillate plant. × 4. (*c*) *C. Webbiana* (Hawaiian plant), habit. × 1.5. (*d*) *C. sertularioides*, habit. × .5. (*e*) *C. sertularioides*, filiform ramulus of frond. × 1.5. (*f*) *C. taxifolia*, habit. × .5. (*g*) *C. taxifolia*, sickle-shaped, mucronate ramulus of frond. × 1.5. (*h*) *C. serrulata* var. *typica* f. *lata*, habit showing serrate infolded margin of frond. × 1.5. (*i*) *C. serrulata* var. *typica* f. *serrulata*, habit showing untwisted frond with regular serrations throughout.

× 1.5. (*j*) *C. serrulata* var. *typica* f. *angusta*, habit showing smooth inrolled margins of frond. × 1.5. (*k*) *C. lentillifera*, ramulus of frond showing constriction of pedicel at base of globose apex. × 5. (*l*) *C. lentillifera*, habit. × 1. (*m*) *C. racemosa* var. *microphysa*, habit. × 1.5. (*n*) *C. racemosa* var. *macrophysa*, habit. × .7. (*o*) *C. racemosa* var. *turbinata*, ramulus of frond showing trumpet-like profile. × 10. (*p*) *C. racemosa* var. *turbinata*, habit of frond with adjacent young branch exhibiting "laete-viroid" structure. × 3. (*q*) *C. racemosa* var. *turbinata*, habit, ramular proliferation. × 1. (*r*) *C. racemosa* var. *peltata*, habit. × .7. (*s*) *C. racemosa* var. *peltata*, portion of frond showing peltate ramulus. × 3. (*t*) *C. racemosa*, variety unclassifiable owing to diversity of ramular types on a single rhizome. Such transition plants are abundant in Hawaii. × 1. (*u*) *C. racemosa* var. *exigua*, habit with proliferating ramulus. × 4. (*v*) *C. racemosa* var. *exigua*, prostrate habit, with proliferating ramuli. × 1. (*w*) *C. racemosa* var. *imbricata*, habit. × 1.5.

PLATE 22

Caulerpa ambigua (photomicrographs taken of material preserved in formalin):

Fig. *a.* Var. *simplex* type (coll: Papenfuss 10507*a*). Habit of frond with simple ramuli. × 14.3.

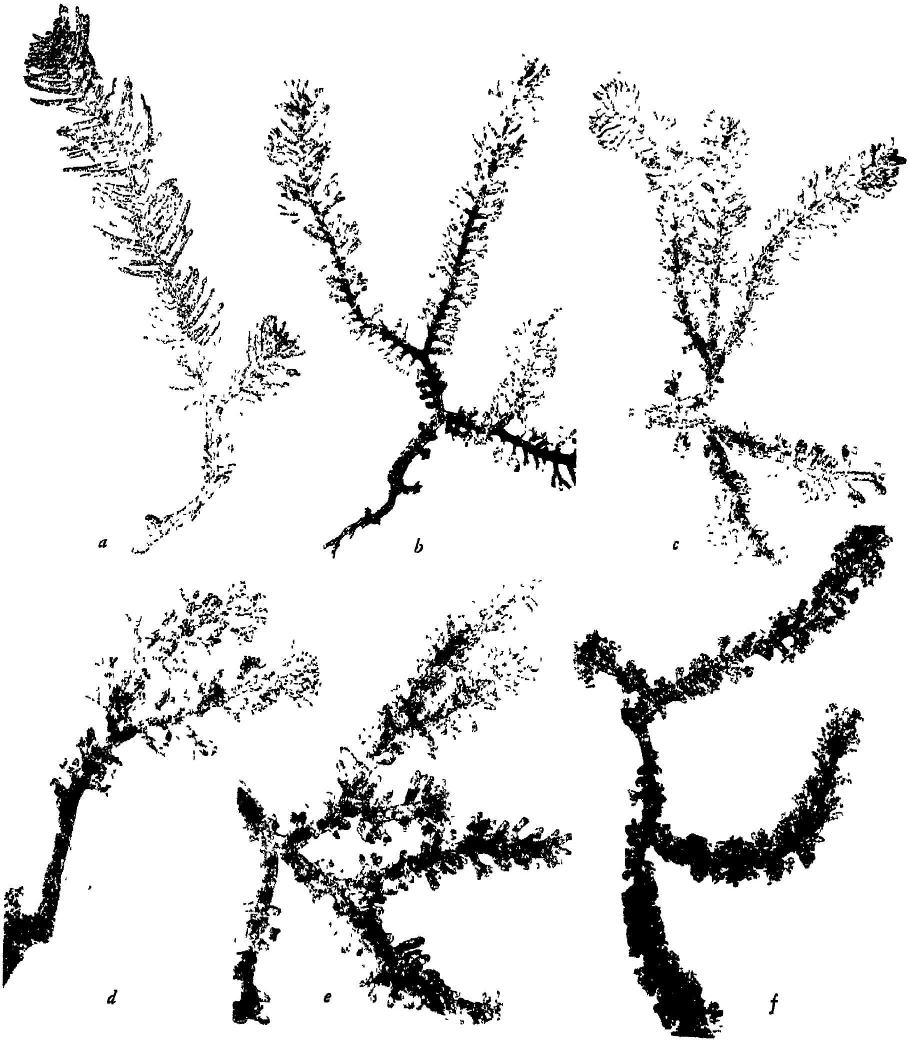
Fig. *b.* Var. *dichotoma,* type (coll: Eubank 627). Habit of fronds with dichotomous ramuli and portion of rhizome. × 18.

Fig. *c.* Var. *dichotoma* (coll: Eubank 628). Habit of fronds with dichotomous ramuli. × 15.5.

Fig. *d.* Var. *furcifolia* (coll: Eubank 621). Habit of verticillate fronds with furcate ramuli. × 19.

Fig. *e.* Var. *furcifolia* (coll: Eubank 626). Habit of verticillate fronds with furcate ramuli. × 14.3.

Fig. *f.* Var. *furcifolia* (coll: Eubank 620). Habit of multiseriate fronds beset with dwarfed, dense, furcate ramuli. × 14.3.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BY

GEORGE F. PAPENFUSS

AN ATTEMPT was recently made by Papenfuss (1945) to bring some order into the confusion centering about *Acrochaetium, Chantransia* and its subgenus *Grania, Audouinella, Colaconema, Kylinia,* and *Rhodochorton.* It was concluded that on the basis of the type of chromatophore, this complex resolved itself into four genera: namely, *Acrochaetium* Nägeli, *Chromastrum* Papenfuss, *Audouinella* Bory, and *Rhodochorton* Nägeli.

Kylinia and *Colaconema* were regarded as synonymous with *Acrochaetium,* the subgenus *Grania* was considered as synonymous with *Audouinella,* whereas *Chantransia,* as originally understood, did not include species belonging to this complex and thus could be excluded entirely. Further study concerning the identity of *Chantransia* (Papenfuss, 1947) has revealed that it is synonymous with *Oedogonium.*

Since the appearance of the article by Papenfuss on the *Acrochaetium-Rhodochorton* complex, several papers which were published by European phycologists during the war, and which contribute to our knowledge of this group, have become available. The most significant of these is one by Kylin (1944) on the red algae of the west coast of Sweden.

Kylin found that the type species of *Kylinia, K. rosulata,* possessed a stellate chromatophore. Previous information concerning the form of the chromatophore of this species was based upon the observations of Rosenvinge (1909), the author of the genus *Kylinia,* and Levring (1937). According to both these authors, the chromatophore seemed to be parietal in form. For this reason the genus *Kylinia* was merged in *Acrochaetium* by Papenfuss and a new genus *Chromastrum* was erected for those species of this complex which contained one or more stellate chromatophores.

If, as the present author believes, the type of chromatophore constitutes the chief criterion for separation of genera, within this group of algae, it is clear that *Kylinia* should replace *Chromastrum.*

Kylin, however, retains *Kylinia* on the basis of the single basal cell of the type species. According to this method of classification, the genus thus includes species of both *Acrochaetium* and *Chromastrum* as characterized by Papenfuss.

Although the type of basal structure has proved very useful in the grouping of species into sections within this complex, it would seem that the type of chromatophore offers a more dependable criterion for separation into genera. It is proposed, therefore, to refer to *Kylinia* all species with one or more stellate chromatophores, irrespective of the type of base.

As is true of certain other groups of plants, the basal structure must be suspected of being, at least in some degree, adaptive to the substratum. Moreover, there is within this complex a variety of species in which the original spore always retains its identity, as it does in *Kylinia rosulata,* even though it gives rise upon germination to different kinds of filaments. Thus there are species in which all the filaments that issue from the spore are prostrate; in others all are erect; in a third type some of the filaments are prostrate and some erect; and in still others one or more filaments grow downward into the tissues of the host and function as rhizoids. Species of the latter type, such as *Acrochaetium occidentale* Børgesen (1915, p. 44), or even *A. unipes* Børgesen (1915, p. 35), whose single basal cell is partly embedded in the host, would apparently be excluded from *Kylinia* by Kylin.

In his paper on the red algae of Sweden, Kylin also contributes new information on *Colaconema Bonnemaisoniae,* which is the type species of the genus *Colaconema.* According to him, the monospores of this species are formed in clusters, and at times successive cells may become transformed into spores. If the plant studied by Kylin is actually *C. Bonnemaisoniae,* then *Colaconema* should not be in the synonymy of *Acrochaetium,* where Papenfuss placed it. But since none of the previous investigators of *Colaconema* has observed this method of spore formation, there may be some question whether the plants studied by Kylin were actually *C. Bonnemaisoniae.* Pending further knowledge concerning this question, it seems justifiable to retain *Colaconema* in the synonymy of *Acrochaetium.*

In addition to the work of Kylin, recent papers by the following European phycologists deal in part with species of the *Acrochaetium-Rhodochorton* complex: Baardseth (1941), Børgesen (1942), Feldmann (1939–1942), Israelson (1942), and Levring (1941, 1942, 1945). To these must be added the papers by Jao (1937, 1940, 1941) and Nagai (1941), which were overlooked by the present author; and to bring the record up to date, it is necessary to incorporate the extensions in geographic distribution of certain species that are reported upon by Taylor (1945) and Tseng (1945).

In the following list, the number preceding each species is the one that was given to it in the first paper (Univ. Calif. Publ. Bot. 18 (14), 1945). Additions to the original catalogue are arranged in alphabetical sequence under the group to which they belong and are assigned a letter appended to the number of the preceding species. At the end of the paper there is an index of all the species and synonyms that are mentioned in both reports.

Acrochaetium Näg.

Remarks: *Kylinia* Rosenvinge is to be excluded from the synonymy of the genus; and the reference to *A. rosulatum* in the diagnosis is to be deleted.

1. *Acrochaetium affine* Howe et Hoyt. *Kylinia affinis* (Howe et Hoyt) Kylin, 1944: 13.
3. *Acrochaetium Battersianum* Hamel. *Kylinia Battersiana* (Hamel) Kylin, 1944: 13.

4*a*. *Acrochaetium candelabrum* Børgesen, 1942 : 8, figs. 1, 2.
Geogr. distr.: Mauritius on *Sphacelaria*.

5. *Acrochaetium catenulatum* Howe. *Kylinia catenulata* (*Howe*) Kylin, 1944 : 13.
Geogr. distr.: Add: New Zealand (Stewart Island) on *Griffithsia*, Juan Fernandez Islands on various algae.

6. *Acrochaetium Dufourii* (Collins) Børgesen. *Kylinia Dufourii* (Collins) Kylin, 1944 : 13.

10. *Acrochaetium gynandrum* (Rosenv.) Hamel. *Kylinia gynandra* (Rosenv.) Kylin, 1944 : 13.

12. *Acrochaetium Hoytii* Collins. *Kylinia Hoytii* (Collins) Kylin, 1944 : 13.

14. *Acrochaetium rosulatum* (Rosenv.) Papenfuss.
Remarks: This is the type species of the genus *Kylinia* and it should be removed to that genus (see no. 14*a*, p. 437).

16. *Acrochaetium Sargassi* Børgesen. *Kylinia Sargassi* (Børg.) Kylin, 1944 : 13.

18. *Acrochaetium simplex* (Drew) Papenfuss. *Kylinia simplex* (Drew) Kylin, 1944 : 13.

20. *Acrochaetium subpinnatum* Bornet ex Hamel. *Kylinia subpinnata* (Bornet) Kylin, 1944 : 13.

21. *Acrochaetium trifilum* (Buff.) Batters. *Kylinia trifila* (Buff.) Kylin, 1944 : 13.

22. *Acrochaetium unilaterale* (Kjellm.) Hamel. *Kylinia unilateralis* (Kjellm.) Kylin, 1944 : 13.

27a. *Acrochaetium Chnoosporae* Børgesen, 1942 : 13, fig. 5.
Geogr. distr.: Mauritius on *Chnoospora*.

31. *Acrochaetium Daviesii* (Dillw.) Nägeli.
Geogr. distr.: Add: Mediterranean on *Cystoseira*, Revilla Gigedo Islands on *Caulerpa*, New Zealand (Stewart Island) on *Griffithsia*, Tristan da Cunha on *Gymnogongrus*, Inaccessible Island on *Cladophora*.

41a. **Acrochaetium kurilense** (Nagai) Papenfuss, comb. nov. *Rhodochorton kurilense* Nagai, 1941 : 156, pl. 4, figs. 23–28.
Geogr. distr.: Kurile Islands on *Chaetomorpha*.

45. *Acrochaetium mahumetanum* Hamel.
Remarks: According to Levring (1942, p. 8) this entity is synonymous with *Chantransia humilis* Rosenvinge [= *Kylinia humilis* (Rosenv.), see p. 437].

45a. *Acrochaetium mauritianum* Børgesen, 1942 : 11, figs. 3, 4.
Geogr. distr.: Mauritius on *Chaetomorpha*.

49. *Acrochaetium pacificum* Kylin.
Geogr. distr.: Add: Juan Fernandez Islands on various algae and *Sertularia*.

58. *Acrochaetium Savianum* (Menegh.) Nägeli.
Geogr. distr.: Add: Mediterranean coast of France on *Posidonia*.

62. *Acrochaetium subseriatum* Børgesen.
Geogr. distr.: Add: Mauritius on *Griffithsia*.

63. *Acrochaetium Thuretii* (Born.) Collins et Hervey.
Geogr. distr.: Add: Juan Fernandez Islands on *Dictyota* and *Splachnidium*.

76. *Acrochaetium Bonnemaisoniae* (Batt.) J. et G. Feldmann.
Remarks: See the account of Kylin (1944, p. 29).

86a. *Acrochaetium Drewiae* Baardseth, 1941: 43, fig. 19 A–D.
Geogr. distr.: Nightingale Island in *Laminaria.*

89a. *Acrochaetium endophyticum* Batters var. *tristanense* Baardseth, 1941: 45, fig. 19 E–G.
Geogr. distr.: Tristan da Cunha in *Heterosiphonia.*

90a. *Acrochaetium Erythrophyllum* Jao, 1937: 112, pl. 14, figs. 1–3.
Geogr. distr.: Pacific coast of North America in *Erythrophyllum.*

90b. **Acrochaetium fernandezianum** (Levr.) Papenfuss, comb. nov. *Chantransia fernandeziana* Levring, 1941: 631, fig. 10 I–R.
Geogr. distr.: Juan Fernandez Islands in *Dictyota.*

90c. **Acrochaetium grandis** (Levr.) Papenfuss, comb. nov. *Chantransia grandis* Levring, 1941: 632, fig. 10 A–H.
Geogr. distr.: Juan Fernandez Islands in various algae.

102a. **Acrochaetium Levringii** Papenfuss, nom. nov. *Acrochaetium microfilum* Levring, 1945: 12, fig. 4 (not of Jao, 1936).
Geogr. distr.: Tierra del Fuego (Staten Island) in *Desmarestia.*

114. *Acrochaetium penetrale* (Drew) Papenfuss.
Geogr. distr.: Add: Pacific coast of Costa Rica in *Zoöbotrys.*

115. *Acrochaetium penetrans* (Levr.) Papenfuss.
Remarks: According to Kylin (1944, p. 21), this entity is synonymous with *Audouinella pectinata* (see Papenfuss, 1945, p. 326).

122. *Acrochaetium rhizoideum* (Drew) Jao.
Remarks: This combination was first made by Jao (1937, p. 102).

123. *Acrochaetium robustum* Børgesen.
Geogr. distr.: Add: Hong Kong in *Sargassum.*

130. *Acrochaetium vagum* (Drew) Jao.
Remarks: This combination was first made by Jao (1937, p. 111).

Kylinia Rosenv.

Rosenvinge, 1909: 141; Kylin, 1944: 12 (in part). *Chromastrum* Papenfuss, 1945: 320.

Type species: *Kylinia rosulata* Rosenvinge.

1. *Kylinia Alariae* (Jónss.) Kylin, 1944: 13.

2. *Kylinia arcuata* (Drew) Kylin, 1944: 13. *Acrochaetium arcuatum* (Drew) Tseng, 1945: 158, pl. 1, fig. 1.
Geogr. distr.: Add: Hong Kong on *Chaetomorpha.*

3. **Kylinia baltica** (Rosenv.) Papenfuss, comb. nov. *Chantransia baltica* Rosenvinge, 1909: 97.

4. *Kylinia collopoda* (Rosenv.) Kylin, 1944: 15.

5. **Kylinia compacta** (Jao) Papenfuss, comb. nov. *Acrochaetium compactum* Jao, 1936: 241.

6. *Kylinia crassipes* (Børgs.) Kylin, 1944: 13.

6a. **Kylinia curta** (Baards.) Papenfuss, comb. nov. *Acrochaetium curtum* Baardseth, 1941: 40, fig. 16 E–H.
Geogr. distr.: Tristan da Cunha on *Polysiphonia.*

7. *Kylinia hallandica* (Kylin) Kylin, 1944: 15.

8. *Kylinia hirsuta* (Drew) Kylin, 1944: 13.
9. *Kylinia macropus* (Kylin) Kylin, 1944: 13.
10. *Chromastrum maluinum* (Hamel) Papenfuss, 1945: 321.
    Remarks: In the opinion of Kylin (1944, p. 14), this entity is indistinguishable from *Kylinia parvula.*

10a. **Kylinia mediterranea** (Levr.) Papenfuss, comb. nov. *Chantransia mediterranea* Levring, 1942: 6, fig. 1 A–G.
    Geogr. distr.: Mediterranean on *Cladophora.*

11. *Kylinia microscopica* (Näg.) Kylin, 1944: 13.
12. *Kylinia moniliformis* (Rosenv.) Kylin, 1944: 16.
13. *Kylinia parvula* (Kylin) Kylin, 1944: 13.
14. *Chromastrum rhipidandrum* (Rosenv.) Papenfuss, 1945: 322.
    Remarks: According to Kylin (1944, p. 13) this entity is synonymous with *Kylinia parvula.*

14a. *Kylinia rosulata* Rosenvinge, 1909: 141; Kylin, 1944: 12, fig. 3.
    Remarks: The structures which Rosenvinge took for male reproductive organs were hair primordia, according to Kylin. As far as known, the species thus lacks sexual reproduction.

15. **Kylinia unifila** (Jao) Papenfuss, comb. nov. *Acrochaetium unifilum* Jao, 1936: 239.
16. **Kylinia Börgesenii** (Schiffn.) Papenfuss, comb. nov. *Acrochaetium Börgesenii* Schiffner, 1931: 143.
17. **Kylinia Duboscqii** (Feldm.) Papenfuss, comb. nov. *Acrochaetium Duboscqii* Feldmann, 1935: 366; 1939: 213, fig. 6.
18. **Kylinia floridulum** (Dillw.) Papenfuss, comb. nov. *Conferva floridula* Dillwyn, 1802: 73.
    Geogr. distr.: Add: Tristan da Cunha on rocks.

19. **Kylinia humilis** (Rosenv.) Papenfuss, comb. nov. *Chantransia humilis* Rosenvinge, 1909: 117.
    Remarks: According to Levring (1942, p. 8), *Acrochaetium mahumetanum* Hamel (see Papenfuss, 1945, p. 309) is synonymous with *K. humilis.*
    Geogr. distr.: Add: Mediterranean on *Cladophora.*

20. **Kylinia Macula** (Rosenv.) Papenfuss, comb. nov. *Chantransia Macula* Rosenvinge, 1909: 114.
21. **Kylinia polyblasta** (Rosenv.) Papenfuss, comb. nov. *Chantransia polyblasta* Rosenvinge, 1909: 115.
22. **Kylinia pulchella** (Børgs.) Papenfuss, comb. nov. *Acrochaetium pulchellum* Børgesen, 1915: 23.
    Geogr. distr.: Add: Tristan da Cunha on *Streblocladia,* Inaccessible Island on *Dipterosiphonia.*

23. **Kylinia secundata** (Lyngb.) Papenfuss, comb. nov. *Callithamnion Dawiesii β secundatum* Lyngbye, 1819: 129.
    Geogr. distr.: Add: Mediterranean on *Cladophora, Chaetomorpha* and *Zostera.*

24. **Kylinia sessilis** (Nakam.) Papenfuss, comb. nov. *Rhodochorton sessile* Nakamura, 1941: 278.
25. **Kylinia virgatula** (Harv.) Papenfuss, comb. nov. *Callithamnion virgatulum* Harvey, *in* Hooker, 1833: 349.

26. **Kylinia cytophaga** (Rosenv.) Papenfuss, comb. nov. *Chantransia cytophaga* Rosenvinge, 1909 : 121.
    Remarks: Asexual reproduction by mono- and tetraspores.
27. **Kylinia Dumontiae** (Rosenv.) Papenfuss, comb. nov. *Chantransia Dumontiae* Rosenvinge, 1909 : 124.
28. **Kylinia immersa** (Rosenv.) Papenfuss, comb. nov. *Chantransia immersa* Rosenvinge, 1909 : 130.
29. **Kylinia implicata** (Drew) Papenfuss, comb. nov. *Rhodochorton implicatum* Drew, 1928 : 190.
30. **Kylinia infestans** (Howe et Hoyt) Papenfuss, comb. nov. *Acrochaetium infestans* Howe et Hoyt, 1916 : 116.
31. **Kylinia Liagorae** (Børgs.) Papenfuss, comb. nov. *Acrochaetium Liagorae* Børgesen, 1915 : 58.
    Geogr. distr.: Add: Juan Fernandez Islands in *Liagora.*
32. **Kylinia Liagoroides** (Børgs.) Papenfuss, comb. nov. *Acrochaetium Liagoroides* Børgesen, 1937 : 40.
33. **Kylinia Porphyrae** (Drew) Papenfuss, comb. nov. *Rhodochorton Porphyrae* Drew, 1928 : 188.
34. **Kylinia Stilophorae** (Levr.) Papenfuss, comb. nov. *Chantransia Stilophorae* Levring, 1935: 39. *Acrochaetium Stilophorae* (Levr.) Kylin, 1944 : 25.

Audouinella Bory

Papenfuss, 1945 : 325. *Grania* (Rosenv.) Kylin, 1944 : 26.

Remarks: Some of the species described by Jao (1940, 1941) may be examples of the so-called *Chantransia*-stages of *Batrachospermum* or *Lemanea.*

1. *Audouinella eugenea* (Skuja) Jao.
Remarks: This combination was first made by Jao (1940, p. 243).

1a. *Audouinella cylindrica* Jao, 1941 : 252, pl. 3, fig. 15.
Geogr. distr.: China (near Yangso City, Kwangsi) on *Vallisneria spiralis.*

1b. *Audouinella glomerata* Jao, 1941 : 254, pl. 3, figs. 18–20.
Geogr. distr.: China (in a mountain stream near Pehpei, Szechwan) on rocks and aquatics.

2a. *Audouinella lanosa* Jao, 1941 : 256, pl. 3, figs. 16, 17.
Geogr. distr.: China (near Pehpei, Szechwan) on the concrete wall of a dam.

3a. *Audouinella sinensis* Jao, 1940 : 241, pl. 1, figs. 5, 6; 1941 : 257.
Geogr. distr.: China (Pei-lung-tang and Nanyoh) on rocks.

4. *Audouinella subtilis* (Möb.) Jao.
Remarks: This combination was first made by Jao (1941, p. 253).

6. *Audouinella violacea* (Kütz) Hamel.
Remarks: Israelson (1942, p. 15) considers *A. violacea* as synonymous with *A. Hermanni* or *Chantransia Hermanni,* as he calls it.

7. *Audouinella efflorescens* (J. Ag.) Papenfuss, 1945 : 326. *Grania efflorescens* (J. Ag.) Kylin, 1944 : 26.

8. *Audouinella membranacea* (Magnus) Papenfuss, 1945 : 326.
Geogr. distr.: Add: Mediterranean on sponges.

9. *Audouinella pectinata* (Kylin) Papenfuss, 1945 : 326.

Remarks: According to Kylin (1944, p. 21), ***Chantransia penetrans*** Levring is synonymous with ***A. pectinata.***

Rhodochorton Näg.

Papenfuss, 1945 : 327.

1a. *Rhodochorton bisporiferum* Baardseth, 1941 : 47, figs. 20 A–C, 21B.

Geogr. distr.: Inaccessible Island on rocks.

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INDEX

Acrochaetium affine, 305, 434
  Alariae, 320
  Alcyonidii, 312
  americanum, 312
  Amphiroae, 312
  angustum, 312
  antillarum, 312
  arcuatum, 436
  Arnoldii, 312
  Asparagopsis, 312
  attenuatum, 308
  Avrainvilleae, 312
  bahreinii, 305
  barbadense, 312
  Battersianum, 306, 434
  bisporum, 312
  Bonnemaisoniae, 312, 435
  Børgesenii, 322, 437
  Bornetii, 313
  botryocarpum, 313
  Brebneri, 313
  bulbosum, 313
  caesareae, 306
  caespitiforme, 308
  caespitosum, 308
  canariense, 308
  candelabrum, 435
  catenulatum, 306, 435
  Chnoosporae, 435
  Chylocladiae, 313
  clandestinum, 308
  coccineum, 313
  Codicola, 313
  Codii, 314
  Collinsianum, 324
  collopodum, 321
  compactum, 321, 436
  comptum, 314
  corymbiferum, 313
  crassipes, 321
  curtum, 436
  Cymopoliae, 308
  cytophagum, 324
  Dasyae, 308
  Daviesii, 308, 435
  densum, 308
  Desmarestiae, 308
  Dictyotae, 314
  discoideum, 309
  Drewiae, 436
  Duboscqii, 322, 437
  Dufourii, 306, 435
Acrochaetium Dumontiae, 324
  dwarkense, 306
  Eastwoodae, 306
  efflorescens, 326
  elegans, 314
  emergens, 314
  endophyticum, 314
  endophyticum var. tristanense, 436
  endozoicum, 314
  erectum, 306
  ernothrix, 318
  Erythrophyllum, 436
  fernandezianum, 436
  flexuosum, 309
  fuegiense, 309
  globosum, 309
  gracile, 309
  grandis, 436
  Griffithsianum, 319
  Gymnogongri, 318
  gynandrum, 306, 435
  hallandicum, 321
  Hameli, 314
  Hancockii, 306
  Hauckii, 329
  hormorhizum, 314
  Howei, 314
  Hoytii, 306, 435
  humile, 323
  Hyalosiphoniae, 314
  Hypneae, 314
  inclusum, 315
  immersum, 324
  infestans, 324, 438
  intermedium, 315
  interpositum, 315
  Iyengarii, 309
  japonicum, 315
  Jónssonii, 309
  krusadii, 309
  Kuckuckianum, 315
  kurilense, 435
  Kylinii, 315
  lanuginosum, 319
  Lauterbachii, 315, 317
  Lenormandi, 309
  Leptonema, 309
  Levringii, 436
  Liagorae Børg., 324, 438
  Liagorae Hamel, 318
  Liagoraefilum, 315
  Liagoroides, 325, 438

Acrochaetium Lorrain-Smithiae, 309
  macropus, 321
  Macounii, 315
  Macula, 323
  magnificum, 316
  mahumetanum, 309, 435, 437
  maluinum, 321
  mauritianum, 435
  microfilum Jao, 306
  microfilum Levr., 436
  microscopicum, 322
  minimum, 316
  minutissimum, 310
  minutum, 310
  molle, 318
  moniliforme, 322
  multisporum, 316
  Naumannii, 316
  Nemalionis, 316
  netrocarpum, 310
  Nitophylli, 316
  obscurum, 316
  occidentale, 316
  opetigenum, 316
  pacificum, 310, 435
  pallens, 310
  parvulum, 322
  pectinatum, 326
  penetrale, 316, 436
  penetrans, 316, 436
  phacelorhizum, 317
  plumosum, 310
  polyblastum, 323
  Polyidis, 317
  polyrhizum, 317
  polysporum, 310
  Porphyrae, 325
  pulchellum, 323, 437
  Pubes, 319
  pulvereum, 319
  radians, 310
  radiatum, 310
  radicans, 319
  Ralfsiae, 317
  reductum, 311
  repens, 309, 317
  reticulatum, 317
  rhipidandrum, 322
  rhizoideum, 317, 436
  robustum, 317, 436
  rosulatum, 307, 435
  ryukyuense, 307
  Sagraeanum, 311
  sanctae-mariae, 317
Acrochaetium sancti-thomae, 311
  Sargassi, 307, 435
  Sargassicolum, 317
  Savianum, 311, 435
  scapae, 307
  secundatum, 323
  seiriolanum, 311
  seriatum, 311
  simplex, 307, 435
  sinicolum, 317
  sparsum, 310, 318
  Spathoglossi, 307
  spongicolum, 317
  Stilophorae, 438
  strictum, 311
  subimmersum, 318
  subpinnatum, 307, 435
  subseriatum Børg., 311, 435
  subseriatum Jao, 307
  subtillissimum, 318
  tenuissimum, 319
  Thuretii, 311, 435
  trifilum, 307, 435
  tuticorinense, 311
  unifilum, 322, 437
  unilaterale, 307, 435
  unipes, 318
  vagum, 318, 436
  Vanbosseae, 318
  variabile, 311
  virgatulum, 323
  virgatulum f. tenuissima, 319
  Zosterae, 307
Audouinella Boweri, 326
  cylindrica, 438
  efflorescens, 326, 438
  eugenea, 325, 438
  glomerata, 438
  Hermanni, 325, 438
  lanosa, 438
  membranacea, 326, 438
  mstinensis, 325
  pectinata, 326, 436, 439
  sinensis, 438
  subtilis, 325, 438
  tenella, 326
  violacea, 326, 438
Byssus purpurea, 327
Callithamnion corynosporoides, 327
  Dawiesii β secundatum, 323, 437
  efflorescens, 326
  membranaceum, 326
  microscopicum, 322
  minutissimum, 310

Callithamnion minutum, 310
  sparsum, 310, 318
  virgatulum, 323, 437
Chantransia Alariae, 320
  ascosperma, 319
  attenuata, 308
  baltica, 321, 436
  Bonnemaisoniae, 312
  Boweri, 326
  chiloensis, 319
  Codii, 314
  collopoda, 321
  concava, 319
  corymbifera, 313
  crassipes, 321
  cytophaga, 324, 438
  Daviesii, 308
  Dufourii, 306
  Dumontiae, 324, 438
  efflorescens, 326
  efflorescens var. Thuretii, 311
  emergens, 314
  endozoica, 314
  eugenea, 325
  fernandeziana, 436
  flagellifera, 319
  gracillima, 320
  grandis, 436
  gynandra, 306
  hallandica, 321
  Hermanni, 438
  humilis, 323, 435, 437
  immersa, 324, 438
  inclusa, 315
  interposita, 315
  irregularis, 320
  Lauterbachii, 315
  leptonema, 309
  Liagorae Børg., 324
  Liagorae, Web. v. Bosse, 318
  Lorrain-Smithiae, 308, 309
  Macounii, 315
  Macula, 323, 437
  mediterranea, 437
  microscopica, 306
  microscopica var. collopoda, 321
  microscopica var. pygmaea, 315
  mirabilis, 315
  mollis, 318
  moniliformis, 322
  mstinensis, 325
  Nemalionis, 316
  Nitophylli, 316
  Nordstedtiana, 320
Chantransia parvula, 322
  pectinata, 326
  penetrans, 316, 439
  polyblasta, 323, 437
  Polyidis, 317
  reducta, 311
  rhipidandra, 322
  rigida, 320
  sanctae-mariae, 317
  secundata, 319, 323
  Stilophorae, 325, 438
  stricta, 311
  subtilis, 325
  tenella, 326
  tenuissima, 319
  Thuretii, 311
  trifila, 307
  unilateralis, 307
  velutina, 319
  vinculoides, 320
  violacea, 326
  virgatula, 323
  virgutula f. tenuissima, 319
Chromastrum Alariae, 320
  arcuatum, 321
  balticum, 321
  Boergesenii, 322
  collopodum, 321
  compactum, 321
  crassipes, 321
  cytophagum, 324
  Duboscqii, 322
  Dumontiae, 324
  floridulum, 323
  hallandicum, 321
  hirsutum, 321
  humile, 323
  immersum, 324
  implicatum, 324
  infestans, 324
  Liagorae, 324
  Liagoroides, 325
  macropus, 321
  Macula, 323
  maluinum, 321, 437
  microscopicum, 322
  moniliforme, 322
  parvulum, 322
  polyblastum, 323
  Porphyrae, 325
  pulchellum, 323
  rhipidandrum, 322, 437
  secundatum, 323
  sessile, 323

- Chromastrum Stilophorae, 325
  - unifilum, 322
  - virgatulum, 323
- Colaconema americana, 312
  - Asparagopsis, 312
  - Bonnemaisoniae, 312
  - Chylocladiae, 313
  - ? reticulatum, 317
  - simplex, 315
- Conferva floridula, 323, 437
  - Rothii, 327
  - violacea, 327
- Grania efflorescens, 438
- Kylinia affinis, 434
  - Alariae, 436
  - arcuata, 436
  - baltica, 436
  - Battersiana, 434
  - Børgesenii, 437
  - catenulata, 435
  - collopoda, 436
  - compacta, 436
  - crassipes, 436
  - curta, 436
  - cytophaga, 438
  - Duboscqii, 437
  - Dufourii, 435
  - Dumontiae, 438
  - floridulum, 437
  - gynandra, 435
  - hallandica, 436
  - hirsuta, 437
  - Hoytii, 435
  - humilis, 435, 437
  - immersa, 438
  - implicata, 438
  - infestans, 438
  - Liagorae, 438
  - Liagoroides, 438
  - macropus, 437
  - Macula, 437
  - mediterranea, 437
  - microscopica, 437
  - moniliformis, 437
  - parvula, 437
  - polyblasta, 437
  - Porphyrae, 438
  - pulchella, 437
  - rosulata, 307, 436, 437
  - Sargassi, 435
  - scapae, 307
  - secundata, 437
  - sessilis, 437
  - simplex, 435
- Kylinia Stilophorae, 438
  - subpinnata, 435
  - trifila, 435
  - unifila, 437
  - unilateralis, 435
  - virgatula, 437
- Pleonosporium constrictum, 329
- Spermothamnion speluncarum, 329
- Rhodochorton affine Yamada, 314
  - affine Drew, 314
  - Amphiroae, 312
  - angustum, 312
  - arcuatum, 321
  - bisporiferum, 439
  - Brebneri, 313
  - catenulatum, 306
  - coccineum, 313
  - concrescens, 327
  - constrictum, 329
  - corymbiferum, 313
  - corynosporoides, 327
  - densum, 308
  - Desmarestiae, 308
  - Dictyotae, 314
  - Eastwoodae, 306
  - efflorescens, 326
  - elegans, 314
  - endophyticum, 315
  - floridulum, 323
  - Galaxaurae, 329
  - Gymnogongri, 318
  - Hancockii, 306
  - Hauckii, 329
  - hirsutum, 321
  - Howei, 314
  - Hyalosiphoniae, 314
  - implicatum, 324, 438
  - intermedium, 327
  - islandicum, 327
  - kurilense, 435
  - Macounii, 315
  - magnificum, 316
  - membranaceum, 326
  - microscopicum, 322
  - minutum, 310
  - moniliforme, 322
  - obscurum, 316
  - pacificum, 310
  - parasiticum, 327
  - penetrale, 316
  - penicilliforme, 327
  - plumosum, 310
  - Porphyrae, 325, 438
  - purpureum, 327

Rhodochorton repens, 309
  rhizoideum, 317
  robustum, 317
  Rothii, 327
  ryukyuense, 307
  sancti-thomae, 311
  seiriolanum, 311
  sessile, 323, 437
  simplex, 307, 315
  sinicola, 317
  speluncarum, 329
  spetsbergense, 328

Rhodochorton subimmersum, 318
  subsimplex, 328
  tenue, 328
  tenuissimum, 319
  vagum, 318
  variabile, 311
  velutinum, 310
  violaceum, 326
  Welwitschii, 329
Thamnidium intermedium, 327
  spetsbergense, 328

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BY

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CHROMOSOME NUMBERS IN THE HYDROPHYLLACEAE: III

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MARION S. CAVE AND LINCOLN CONSTANCE

THIS PAPER is a continuation of our investigation, interrupted by the war, of chromosome numbers in the Hydrophyllaceae. In the two preceding papers of this series* counts were reported for sixty-six species and varieties in the genera *Emmenanthe*, *Eucrypta*, *Hydrophyllum*, *Nemophila*, *Phacelia*, *Pholistoma*, and *Romanzoffia*. The present paper supplements the list with fifty additional species and varieties, including representatives of the genera *Draperia*, *Ellisia*, *Eriodictyon*, *Miltitzia*, *Nama*, *Turricula*, and *Wigandia*. Six counts are given for species already reported upon.

The division of labor between the authors has remained as before. The use of the same acetocarmine smear technique has been continued. All counts are referable to, and the camera-lucida drawings are mounted on, specimens in the University of California Herbarium. Field work has been substantially supplemented by growing various species in the greenhouse. We are very much indebted to Mr. Clarence R. Quick, Bureau of Entomology and Plant Quarantine, Agricultural Research Administration, United States Department of Agriculture, for undertaking the germination of seeds in connection with his studies of seed germination in native plants. Mr. Ernest Jund, Division of Genetics, and Mr. John Whitehead, University of California Botanical Garden, have been of great assistance in the propagation of certain species. Professor E. B. Babcock, Division of Genetics, has generously made greenhouse space available for our project.

We are sincerely grateful to the many correspondents who have supplied us with much of the material from which these counts have resulted, and who have thus enabled us to extend the geographical boundaries of our research. How dependent upon them we have been is indicated by the extensive roster of collectors given in table 1. We hope that we may expand our study through their continued interest and that of others so situated as to be able to secure seeds, propagules, or buds otherwise unobtainable by us.

In *Phacelia* the occurrence of species with five, seven, fourteen, and twenty-four pairs of chromosomes, respectively, has not been reported previously. Plants of *P. Lemmoni* with twenty-two pairs of chromosomes are not dissimilar morphologically from those having twenty-four pairs. This species is evidently a polyploid with aneuploid forms. Because of their close resemblance it was not anticipated that *P. suffrutescens* (10 pairs) would differ in chromosome number from *P. ramosissima* (11 pairs), nor *P. pratensis* (11 pairs) from *P. Davidsonii* (10 pairs).

Some counts are now available for each of the six sections of *Phacelia* recognized by Brand (1913). We have recorded eleven-paired species in all of these except section Cosmanthus, and in all the perennials except *P. suffrutescens* in section Euphacelia and *P. platycarpa* in section Cosmanthus. The appearance of a different numerical pattern in the last-named section suggests that Cosmanthus may not be closely related to the rest of the genus, an indication bolstered by the geographical isolation of the group. From the counts thus far obtained, *Miltitzia* species appear to be uniformly twelve-paired and the species of *Eriodictyon* fourteen-paired.

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* University of California Publications in Botany, vol. 18, nos. 9 and 13.

In earlier taxonomic papers (Constance, 1939*a*, 1939*b*, 1940, 1941) it was proposed to combine *Nemophila aurita* Lindl., *N. racemosa* Nutt. ex A. Gray, and *Ellisia membranacea* Benth. into a distinct genus, *Pholistoma* Lilja. Jepson and Hoover (Jepson, 1943) retained this group of species as circumscribed, but placed it in *Ellisia*. The discovery that *Ellisia Nyctelea* (the type species) has ten pairs of chromosomes, supports the separation of *Pholistoma* from *Ellisia*. Furthermore, all three species of *Pholistoma* show a lagging chromosome at Anaphase I, the possession of which appears to be a distinctive character of the genus, and affords a cytological difference also between *Pholistoma* and *Nemophila*, which agree in chromosome number.

Miltitzia has recently been reduced (Howell, 1944*a*, 1944*b*) to sectional rank under *Phacelia* and placed next to section Microgenetes of the latter genus. It is noteworthy that twelve pairs of chromosomes is the uniform number for the three species of *Miltitzia* examined, and that the two twelve-paired species of *Phacelia* thus far discovered belong to the purportedly related section Microgenetes.

The nearly simultaneous separation of *Phacelia Quickii* (*P. Dociana*) from *P. humilis* by Howell (1942) and by Jepson and Hoover (Jepson, 1943) is abundantly confirmed by the revelation that the two species differ markedly in chromosome number as well as in gross morphology. *Phacelia Quickii* appears to be much more closely related to *P. marcescens* Eastw. (misidentified as *P. irritans* Brand in the first paper of this series), which agrees with it in chromosome number.

Both *Turricula Parryi* and *Nama Lobbii* have been placed, by different authors, in the genus *Eriodictyon*; they have also both been placed in *Nama*. According to C. L. Hitchcock (1933): "*Nama Lobbii* and *N. Parryi* have been considered by such workers as Greene (Bull. Calif. Acad. I: 202. 1885 and Pittonia 2: 22. 1889) and Hall (Univ. Cal. Pub. Bot. I: 106. 1902 and Zoë 5: 265. 1908) to belong to the genus *Eriodictyon*. Of these two species, it seems to the writer that *N. Parryi* should be included under *Eriodictyon* because of the habit, corrugated seeds, corolla (bearded within), and loculicidally and septicidally dehiscent capsules. *Nama Lobbii*, however, may seemingly be most expediently kept in *Nama;* the habit is that of *Nama*, as are the corolla and seed characters. The capsule, which is somewhat cartilaginous and loculicidally and septicidally dehiscent, is an *Eriodictyon*-character, however. It seems wise, therefore, to preserve *N. Lobbii* as a third section or subgenus of *Nama*; it is through *N. Lobbii* and *E. Parryi* that the true relationship of the two genera is manifest." *Turricula Parryi*, with thirteen pairs of chromosomes, differs cytologically from all species studied in either *Eriodictyon* or *Nama*.

Nama Lobbii agrees with *Eriodictyon* in chromosome number, but our investigation of *Nama* will have to be greatly extended before the significance of this fact can be adequately measured.

These few notes concerning the bearing of chromosomal data on specific taxonomic questions may serve to demonstrate the possible applicability of karyological information to problems of relationship. We do not intend to imply that the evidence from chromosome number is necessarily decisive in any of these instances, but it represents a line of attack which can scarcely be ignored in perfecting classification within the family.

FIGURE A

Chromosomes of Ellisia, Pholistoma, Nemophila, Draperia, and Phacelia. × 1150.

1. *Ellisia Nyctelea,* I M; *Constance and McVaugh* (*Gray Herb. Exsic.* 1387).
2. *Pholistoma racemosum,* II T; *H. Lewis* 104.
3. *Nemophila Menziesii* var. *integrifolia,* II M; *K. H. Beach* 1735.
4. *Nemophila Menziesii* var. *atomaria,* II M; *Constance, Ashley, and Mason* 3028.
5. *Nemophila spatulata,* I M; *Constance* 3089.
6. *Draperia systyla,* I A; *Constance and Shan* 3062.
7. *Phacelia Purshii,* I M; *P. R. Stewart.*
8. *Phacelia ranunculacea,* I M; *Constance* 3018.
9. *Phacelia dubia,* I M; *Constance, Bomhard, and Swallen* 3019.
10. *Phacelia hirsuta,* II T; *D. Demaree.*
11. *Phacelia platycarpa,* II M; *T. Morley* 813.
12. *Phacelia viscida,* Diak.; *Constance* 3026.

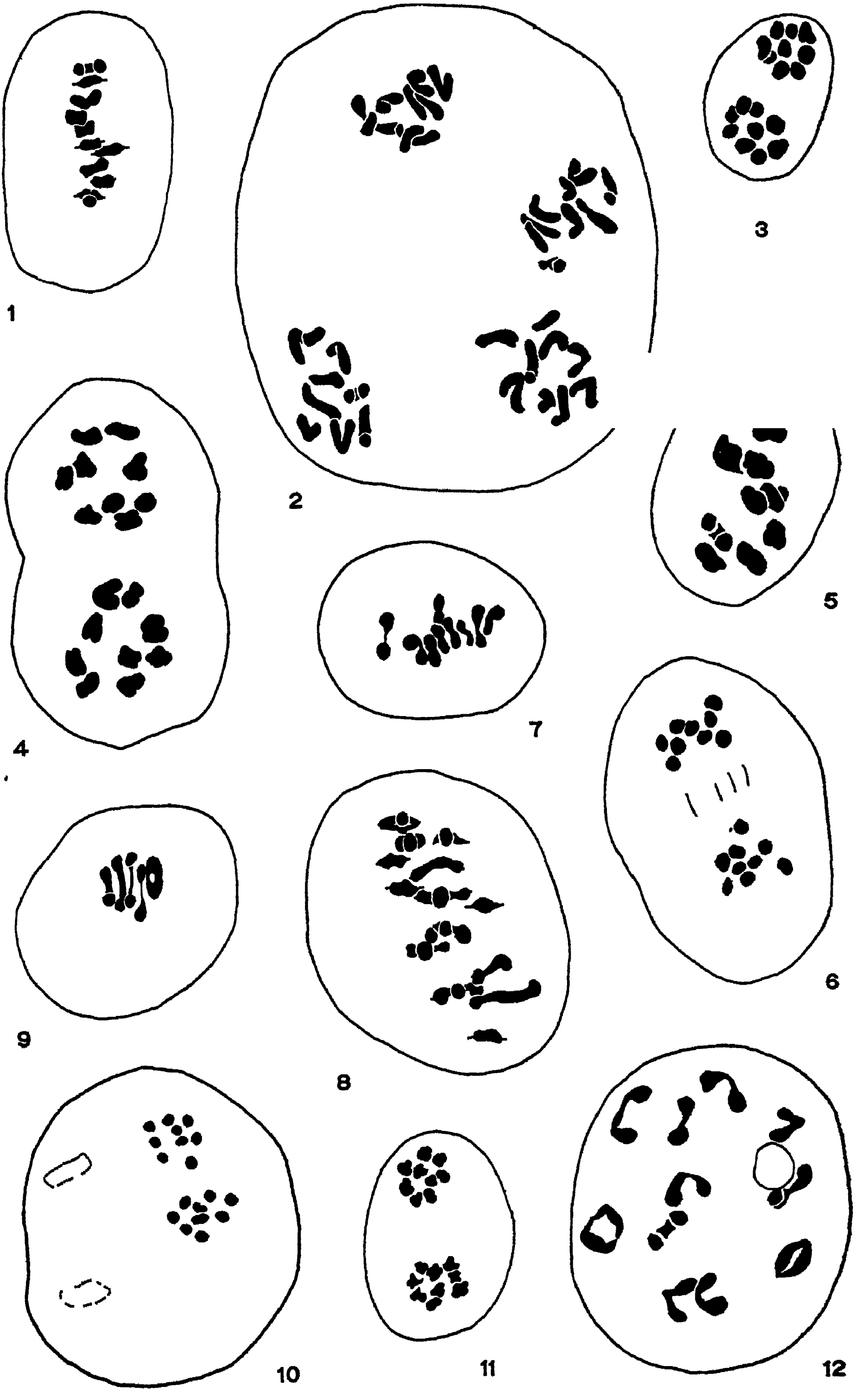

Figure A

FIGURE B

Chromosomes of Phacelia. × 1150.

13. *Phacelia Parryi*, II M; *Constance* 3027.
14. *Phacelia campanularia*, II M; *H. Lewis* 103.
15. *Phacelia coerulea*, II M; *F. W. Gould* 3481.
16. *Phacelia arizonica*, II M; *F. W. Gould* 3052.
17. *Phacelia congesta*, II M; *R. McVaugh* 7525.
18. *Phacelia cicutaria* var. *Hubbyi*, Late Diak.; *C. F. Smith* 1217.
19. *Phacelia ramosissima*, I M; *Constance* 3080.
20. *Phacelia suffrutescens*, Diak.; *K. H. Beach* 1633.
21. *Phacelia Rattani*, I M; *Constance* 3079.
22. *Phacelia nemoralis* (TOPOTYPE), Diak.; *Constance* 3053.
23. *Phacelia compacta*, Diak.; *Alexander and Kellogg*, 3354.

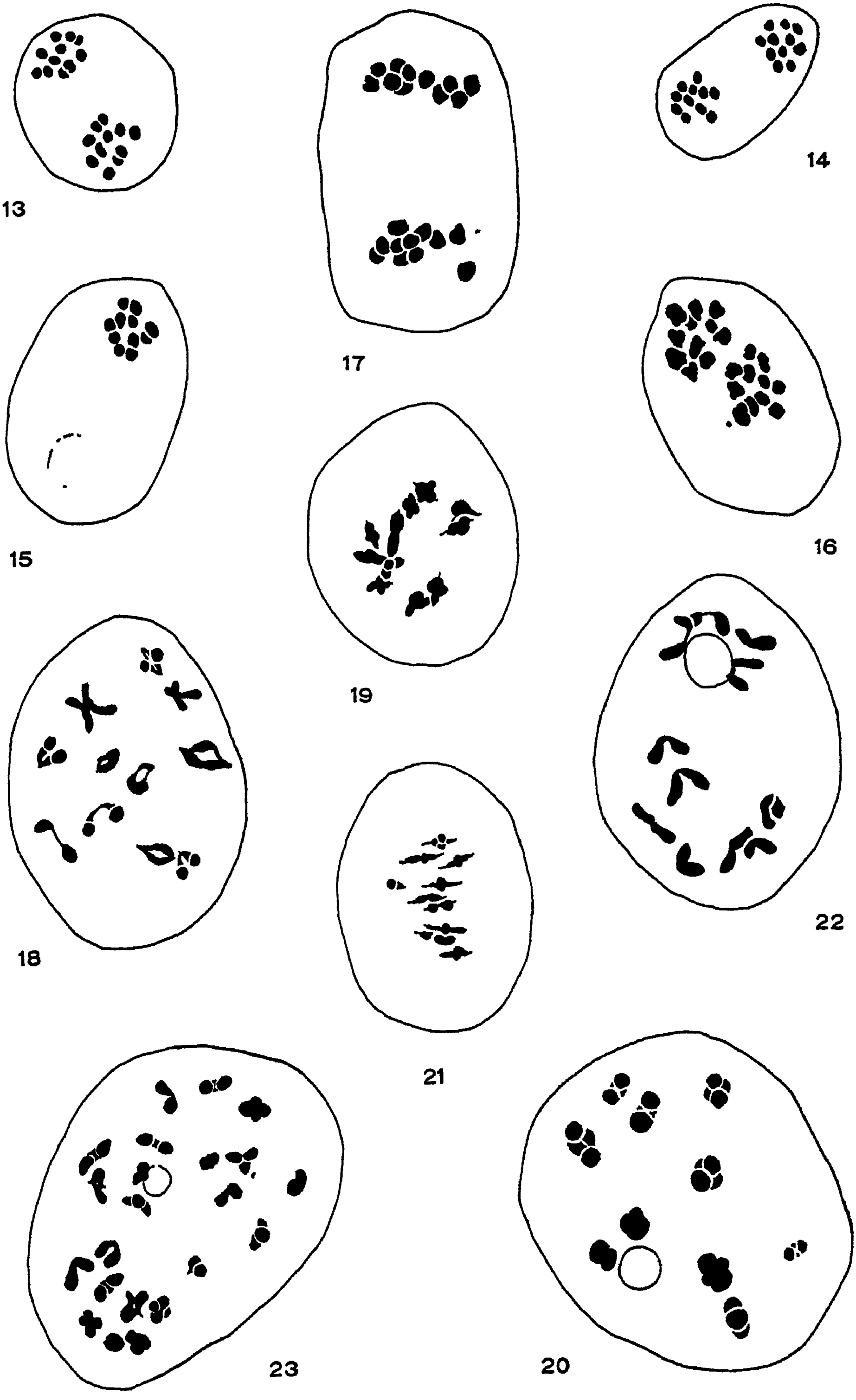

Figure B

FIGURE C

Chromosomes of Phacelia. × 1150.

24. *Phacelia mutabilis* (TOPOTYPE), Diak.; *Constance* 3095.
25. *Phacelia frigida*, II M; *Constance* 3090.
26. *Phacelia urticacea*, II M; *F. W. Gould* 3668.
27. *Phacelia humilis*, II T; *Constance* 3091.
28. *Phacelia Eisenii*, II M; *D. D. Keck* 5316.
29. *Phacelia racemosa*, I M; *Constance* 3087.
30. *Phacelia Quickii*, II M; *C. R. Quick* 42-21.
31. *Phacelia hydrophylloides*, Diak.; *Constance* 3083.
32. *Phacelia pratensis*, Diak.; *A. Carter* 1748.

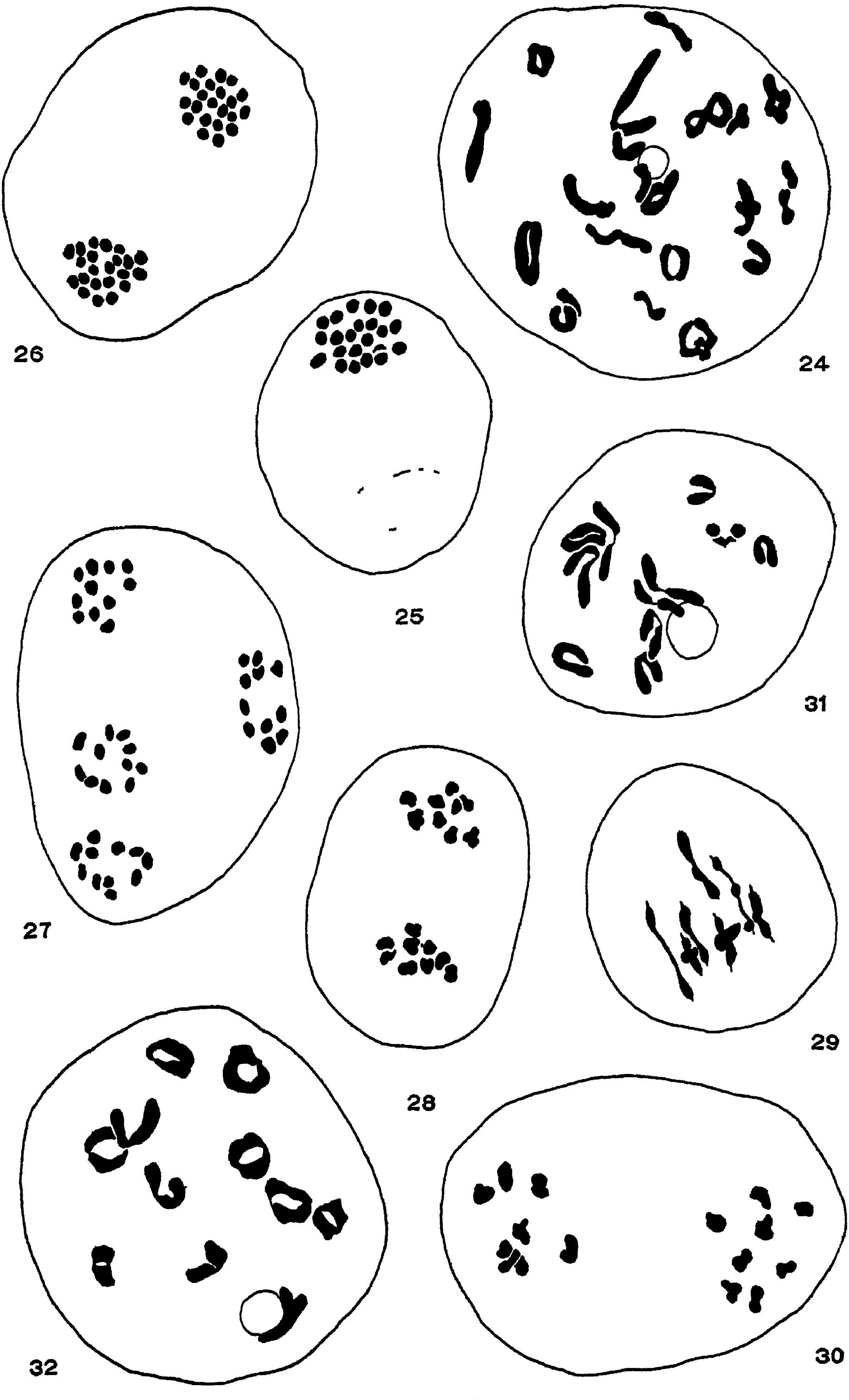

Figure C

FIGURE D

Chromosomes of Phacelia and Romanzoffia. × 1150.

33. *Phacelia Congdoni,* Diak.; *C. B. Wolf* 6735.
34. *Phacelia insularis* var. *continentis,* II M; *Constance, Davidson, Morley, and Shan* 3030.
35. *Phacelia Pringlei,* I M; *Constance and Shan* 3064.
36. *Phacelia phacelioides,* I M; *Constance and Sharsmith* 2574.
37. *Phacelia Lemmonii,* Diak.; *Alexander and Kellogg* 2828.
38. *Phacelia Purpusii,* II M; *G. T. Robbins* 1164.
39. *Phacelia vallicola,* I M; *C. R. Quick* 42-23 (part).
40. *Phacelia affinis* Diak.; *Darrow, Haskell, and Gould* 2963.
41. *Phacelia Cooperae,* I A; *H. L. Mason* 12,841.
42. *Phacelia neglecta,* Diak.; *Eastwood and Howell* 8974.
43. *Romanzoffia Tracyi,* I M; *H. E. Parks* 24,276.

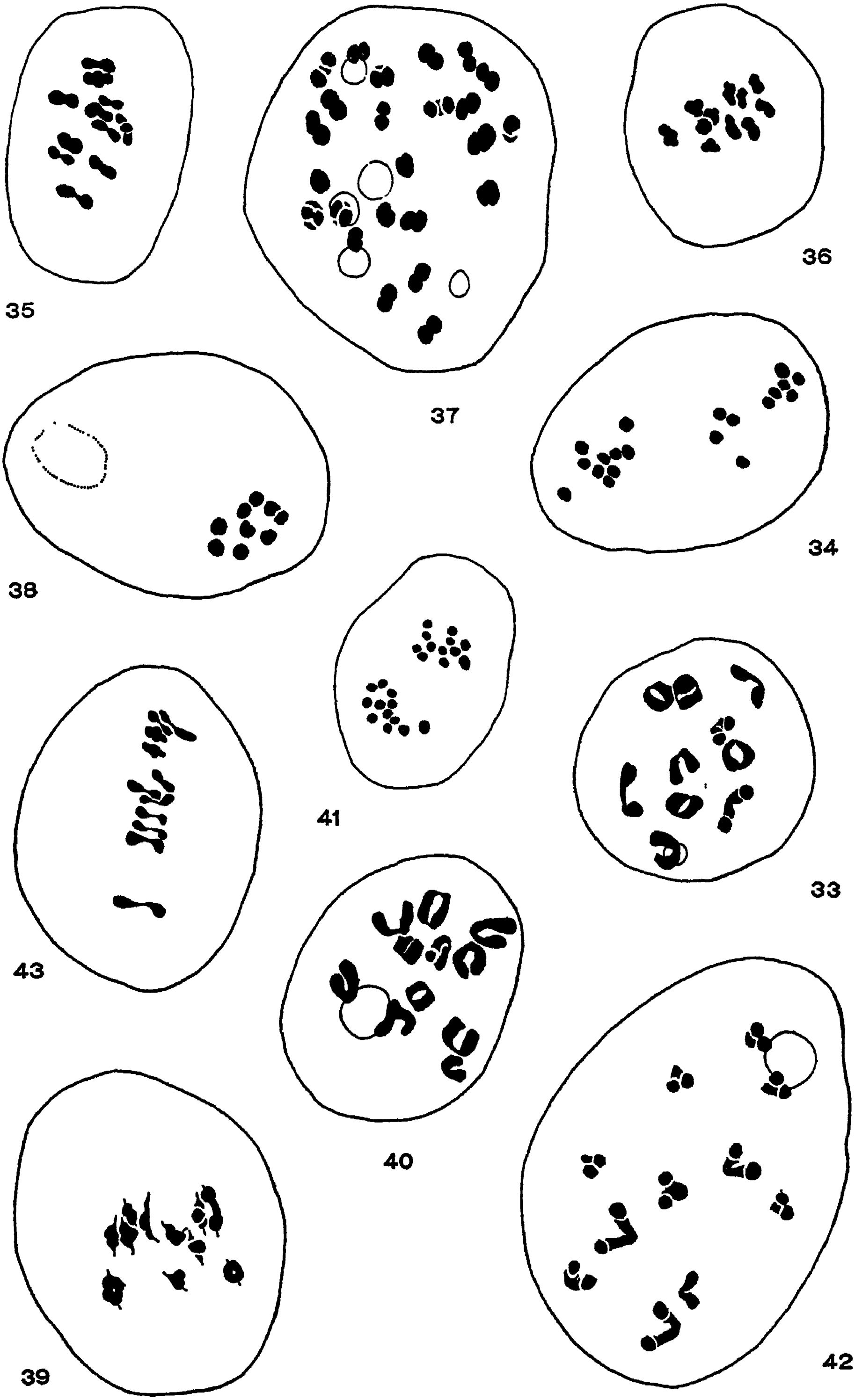

Figure D

FIGURE E

Chromosomes of Miltitzia, Wigandia, Eriodictyon, Turricula, and Nama. × 1150.

44. *Miltitzia lutea* var. ?, Late Diak.; *Alexander and Kellogg* 4538.
45. *Miltitzia parviflora*, Late Diak.; *Constance* 3097.
46. *Miltitzia glandulifera*, Interk.; *Constance* 3100.
47. *Wigandia Kunthii* var. *eu-Kunthii*, Diak.; *J. M. Tucker* 1095.
48. *Eriodictyon crassifolium*, I M; *K. H. Beach* 1743.
49. *Eriodictyon crassifolium* var. *nigrescens*, I M; *K. H. Beach* 1752.
50. *Eriodictyon californicum*, I M; *Signaigo and Morley* 110.
51. *Eriodictyon trichocalyx*, I M; *K. H. Beach* 1747.
52. *Turricula Parryi*, Diak.; *K. H. Beach* 1635.
53. *Nama Lobbii*, I M; *Constance* 3093.
54. *Nama densum* Diak.; *Constance* 3099.
55. *Nama hispidum*, Metaphase of microspore division; *F. W. Gould* 3482.
56. *Nama demissum*, I M; *H. Lewis* 105.

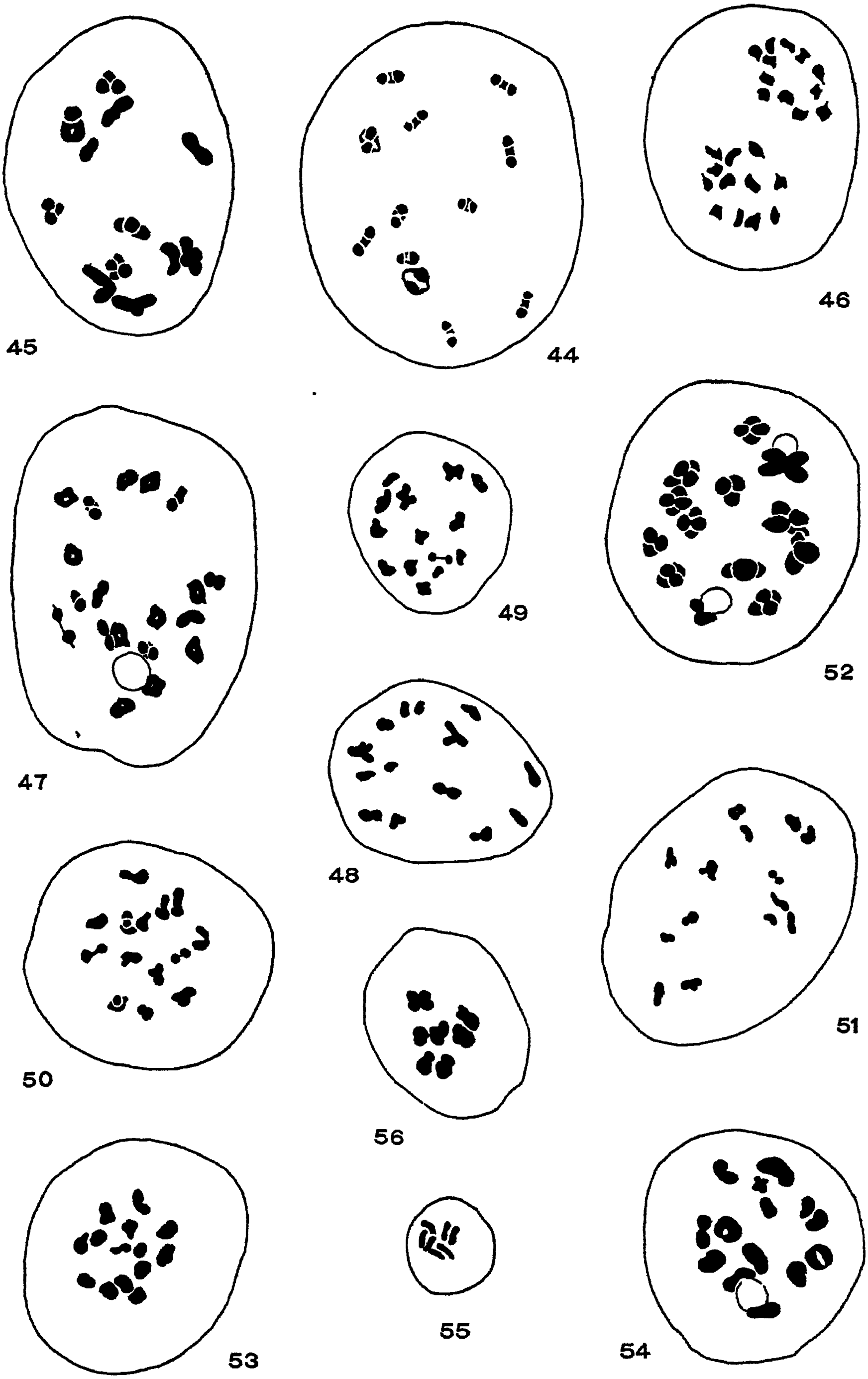

Figure E

TABLE 1

CHROMOSOME NUMBERS IN THE HYDROPHYLLACEAE

Name	n number	Locality	Collector
Ellisia Nyctelea L.	10	Harpers Ferry, Washington Co., Md.	*Constance and McVaugh* (*Gray Herb. Exsic.* 1387)
	10	Shenandoah River, Clarke Co., Va.	*J. T. Baldwin, Jr.* 5590
Pholistoma racemosum (A. Gray) Const.	9	Avalon, Santa Catalina Island, Los Angeles Co., Calif.	*H. Lewis* 104
Nemophila Menziesii H. & A.			
var. *integrifolia* Parish	9	Tanbark Flat, Los Angeles Co., Calif.	*K. H. Beach* 1735
var. *atomaria* (F. & M.) Chandl.	9	Alpine Lake, Marin Co., Calif.	*Constance, Ashley, and Mason* 3028
spatulata Cov.	9	Silver Lake, Amador Co., Calif.	*Constance* 3089
Draperia systyla Torr.	9	Clear Creek, Trinity Co., Calif.	*Constance and Shan* 3062
Phacelia			
Section Cosmanthus			
Purshii Buckl.	9	Glen Echo, Montgomery Co., Md.	*Constance* 3023
	9	Waynesburg, Greene Co., Penna.	*P. R. Stewart*
ranunculacea (Nutt.) Const.	14	Chain Bridge, D. C.	*Constance* 3018
dubia (L.) Trel.	5	Harpers Ferry, Washington Co., Md.	*Constance and McVaugh* (*Gray Herb. Exsic.* 1388)
	5	Plummers Island, Montgomery Co., Md.	*Constance, Bomhard, and Swallen* 3019
hirsuta Nutt.	9	Monticello, Drew Co., Ark.	*D. Demaree*
platycarpa (Cav.) Spreng.	9	Mexico City–Puebla, Mexico	*T. Morley* 813
Section Gymnobythus			
viscida (Benth.) Torr.	11		Theo. Payne's (commercial) strain, *Constance* 3026
Section Whitlavia			
Parryi Torr.	11		Theo. Payne's (commercial) strain, *Constance* 3027
campanularia A. Gray	11	Whitewater Canyon, Riverside Co., Calif.	*H. Lewis* 103

Section Euphacelia			
coerulea Greene	11	Black Mt., Pima Co., Ariz.	*F. W. Gould* 3481
arizonica A. Gray	11	Tucson, Pima Co., Ariz.	*F. W. Gould* 3052
congesta Hook.	11	Coleman, Coleman Co., Texas	*R. McVaugh* 7525
cicutaria Greene			
var. *Hubbyi* (F. Macbr.) J. T. Howell	11	Mission Canyon, Santa Barbara Co., Calif.	*C. F. Smith* 1217
ramosissima Dougl.	11	Felton, Santa Cruz Co., Calif.	*Constance* 3080
	11	Chew's Ridge, Monterey Co., Calif.	*A. A. Beetle* 4300
suffrutescens Parry	10	Corona City, San Bernardino Co., Calif.	*K. H. Beach* 1657
	10	San Dimas, Los Angeles Co., Calif.	*K. H. Beach* 1633
	10	Altadena, Los Angeles Co., Calif.	*H. Lewis* 1720
Rattani A. Gray	11	Felton, Santa Cruz Co., Calif.	*Constance* 3079
magellanica-californica-heterophylla complex			
nemoralis Greene (TOPOTYPE)	11	Berkeley Hills, Alameda Co., Calif.	*Constance* 3053
compacta Greene	22	Cottonwood Lakes, Inyo Co., Calif.	*Alexander and Kellogg* 3354
mutabilis Greene (TOPOTYPE)	22	Summit Station, Placer Co., Calif.	*Constance* 3095
frigida Greene	22	Carson Spur, Amador Co., Calif.	*Constance* 3090
urticacea Greene	22	Sierra Ancha Experimental Forest, Gila Co., Ariz.	*F. W. Gould* 3668
humilis Torr.	11	Luther Pass, Alpine Co., Calif.	*Constance* 3091
Eisenii Brandg.	9	Inspiration Point, Tuolumne Co., Calif.	*D. D. Keck* 5316
racemosa (Kell.) Brandg.	7	Silver Lake, Amador Co., Calif.	*Constance* 3087
Quickii J. T. Howell	8	Strawberry Lake, Tuolumne Co., Calif.	*C. R. Quick* 42-23 (part)
	8	Pinecrest, Tuolumne Co., Calif.	*C. R. Quick* 42-21
	8	Pyramid Ranger Station, Eldorado Co., Calif.	*G. T. Robbins* 1707
Section Eutoca			
hydrophylloides Torr.	11	Silver Lake, Amador Co., Calif.	*Constance* 3083
pratensis Heller	11	Gray's Meadow, Inyo Co., Calif.	*A. Carter* 1748
Congdoni Greene	10	Tejon Ranch, Tejon Canyon, Kern Co., Calif.	*C. B. Wolf* 6735
insularis Munz			
var. *continentis* J. T. Howell	10	Point Reyes, Marin Co., Calif.	*Constance, Davidson, Morley, and Shan* 3030

TABLE 1—*Continued*

Name	n number	Locality	Collector
Phacelia—Continued			
Pringlei A. Gray	11	Carrville, Trinity Co., Calif.	*Constance and Shan* 3064
phacelioides (Benth.) Brand	11	Mt. Diablo, Contra Costa Co., Calif.	*Constance and Sharsmith* 2574
Lemmonii A. Gray	24	Saline Valley, Inyo Co., Calif.	*Alexander and Kellogg* 2828
	24	Hunter Canyon, Inyo Co., Calif.	*Alexander and Kellogg* 2709
Purpusii Brandg.	9	Park Creek road, Eldorado Co., Calif.	*G. T. Robbins* 1164
vallicola Congdon	11	Strawberry Lake, Tuolumne Co., Calif.	*C. R. Quick* 42-23 (part)
Section Microgenetes			
affinis A. Gray	11	Ajo, Pima Co., Ariz.	*Darrow, Haskell, and Gould* 2963
Cooperae A. Gray	12	Big Pine Mt., Santa Barbara Co., Calif.	*H. L. Mason* 12,841
neglecta M. E. Jones	11	Las Vegas, Clark Co., Nev.	*Eastwood and Howell* 8974
Miltitzia			
lutea (H. & A.) A. DC. var. ?	12	Masonic road, Mono Co., Calif.	*Alexander and Kellogg* 4538
glandulifera (Torr.) Heller	12	Termo, Lassen Co., Calif.	*Constance* 3100
parviflora (A. Gray) Brand	12	Eagle Lake, Lassen Co., Calif.	*Constance* 3097
Wigandia Kunthii Choisy			
var. *eu-Kunthii* Brand	19	Los Esesmiles, El Salvador	*J. M. Tucker* 1095
Eriodictyon crassifolium Benth.	14	Lewis Paul Canyon, Los Angeles Co., Calif.	*K. H. Beach* 1743
var. *nigrescens* Brand	14	Johnstone Peak, Los Angeles Co., Calif.	*K. H. Beach* 1752
trichocalyx Heller	14	San Gabriel Mts., Los Angeles Co., Calif.	*K. H. Beach* 1747
californicum (H. & A.) Greene	14	Middletown, Lake Co., Calif.	*Signaigo and Morley* 110
	14	Felton, Santa Cruz Co., Calif.	*Constance* 3081
Turricula Parryi (A. Gray) F. Macbr.	13	Fern Canyon, Los Angeles Co., Calif.	*K. H. Beach* 1635
Nama			
Section Arachnoidea			
Lobbii A. Gray	14	Lake Tahoe, Eldorado Co., Calif.	*Constance* 3093
Section Conanthus			
densum Lemmon	14	Eagle Lake, Lassen Co., Calif.	*Constance* 3099
Section Eunama			
hispidum A. Gray	7	Black Mt., Pima Co., Ariz.	*F. W. Gould* 3482
demissum A. Gray	7	Whitewater Canyon, Riverside Co., Calif.	*H. Lewis* 105
Romanzoffia Tracyi Jepson	11	Trinidad Head, Del Norte Co., Calif.	*H. E. Parks* 24,276

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INDEX

New names and species (as well as titles of contributions to this volume) are printed in **boldface** type.

Acrochaetium. For index of species see pp. 443–444
Acrochaetium-Rhodochorton complex of the red algae, 299 ff., 433 ff.
Actinolepis, 69, 70, 79, 80, 81
  lanosa, 117
  multicaulis, 69, 120
    var. papposa, 120
  nubigena, 115
  Pringlei, 120
  Wallacei, 118
    var. rubella, 118, 119
Aetheorrhiza bulbosa, 235; variants, 239; relationships, 239
Alata-group of Nicotiana. *See* Nicotiana
Altmann freezing-drying technique: method, 23; staining reaction of plant tissues, 24; character of fixation in Lilium longiflorum, 25; value to study, 26, 33; application to plant cytology, 33; anaphase chromosomes in, 34 ff.
Amphiplasty, differential, 373, 392
Amyoplasts, differentiation of mitochondria into, 9, 17
Antheropeas, 70, 79, 80, 81
  australe, 118, 119
  lanosum, 117
  rubellum, 118, 119
  tenuifolium, 117, 118
  Wallacei, 118
Anthocyanols, "coral" vs. "carmine," in Nicotiana Tabacum, 5, 19
Asplenium Clemensiae, 222
  durum, 222
  morobense, 222
  paedigens, 222
Athyrium Archboldii, 222
  decompositum, 222
  latilobum, 222
  minutum, 221
  Myer-Dreesii, 222
  pedicellatum, 222
Audouinella. For index of species see p. 444
Australasian species of Nicotiana. *See* Nicotiana
Avery, Priscilla: **Cytogenetic Evidences of Nicotiana Phylesis in the Alata-group**, 153–194; T. H. Goodspeed, F. M. Uber, and, **Application of the Altmann Freezing-Drying Technique to Plant Cytology. III. Chromosome Structure in Lilium longiflorum**, 33–44

Babcock, E. B., and G. L. Stebbins, **Systematic Studies in the Cichorieae**, 227–240; and J. A. Jenkins, **Chromosomes and Phylogeny in Crepis. III. The Relationships of One Hundred and Thirteen Species**, 241–292
Bahia, 71, 72, 79
  achillaeoides, 87
  ambigua, 116, 117
  arachnoidea, 91, 92
  artemisiaefolia, 112, 113
    var. Douglasii, 112, 113
  confertiflora, 106
    var. trifida, 106, 108
  cuneata, 96
  gracilis, 97, 100, 101, 102, pl. 8
  integrifolia, 96, 97, 100, 102, 108
  lanata, 83, 89
    var. achillaeoides, 87
    var. brachypoda, 91, 92
    var. grandiflora, 89
    var. tenuifolia, 83, 85
  latifolia, 91
  leucophylla, 83, 85, 99, 100, 101, pl. 4
  multiflora, 97, 100
  rubella, 118, 119
  staechadifolia, 112
    var. Californica, 112, 113
  tenuifolia, 106, 108
  trifida, 106, 108
  trollifolia, 91
  Wallacei, 118
Blechnum Brassii, 222
  nudius, 222
Burrielia (Dichaeta) lanosa, 117
Byssus purpurea, 327

Callithamnion. For index of species see pp. 444–445
Calymmodon fragilis, 224
  grammitidiphyllus, 224
  ramifer, 224
Caulerpa, Hawaiian representatives of the genus, 409–431
  ambigua, 410–415, pl. 22
    var. **dichotoma**, 413, 414
    var. **furcifolia**, 413, 414–415
    var. **luxurians**, 414
    var. **simplex**, 413–414, 415
    var. **Vickersiae**, 413, 414
  asplenioides, 409, 417
  Chemnitzia, 409, 421

Caulerpa (*Continued*)
  clavifera, 409, 419
    var. turbinata, 420–421
  crassifolia, 417
  Freycinetii var. typica f. angusta, 418
  lentillifera, 418–419
  peltata, 421, 422, 423
    var. exigua, 422
    var. typica f. imbricata, 423
  Pickeringii, 409, 416
  pinnata, 409, 417
  racemosa, 410, 419–423
    var. Chemnitzia, 420–421
    var. clavifera, 419
    var. **exigua**, 419, 422–423
    var. **imbricata**, 419, 423
    var. laetevirens, 409, 419
    var. macrophysa, 419, 420
    var. microphysa, 419–420
    var. **peltata**, 419, 421–422
    var. **turbinata**, 419, 420–421
  serrulata, 409, 410, 418
    var. typica, 418
      f. **angusta**, 418
      f. lata, 418
      f. serrulata, 418
  sertularioides, 410, 417
  taxifolia, 409, 410, 417
  Vickersiae, 410–415
    var. furcifolia, 411, 412, 414–415
    var. luxurians, 411, 414
  Webbiana, 410, 415–416
    var. **Pickeringii**, 416

Cave, Marion A., and Lincoln Constance, **Chromosome Numbers in the Hydrophyllaceae**, 205–216, 293–298, 449–465
Cells, plant. *See* Cytology
Chantrasia. For index of species see p. 445
Chauvinia imbricata, 423
Cheilanthes belensis, 218
Chiasmata, terminalization of: in Nicotiana of Alata-group, 163 ff.; in Crepis hybrids, 387–388
Chloroplasts, in starch metabolism, 8, 9, 10
Chondriome, of cells in Nicotiana Tabacum, 6, 8
Chromastrum. For index of species see pp. 445–446
Chromatin, in freezing-drying technique, 24, 34, 35, 37
Chromonemata, 33–38 *passim*
Chromosome asymmetry in Crepis: increase in, 242, 269, 273; processes leading to, 269; reciprocal translocations and increase, 269
Chromosome numbers in Crepis: progressive decrease in, 241, 267, 273; most primitive, 267; phylogenetic decrease in, 268–269; dislocation hypothesis, 268, 269; changes in, through translocations, 268–270
Chromosome numbers in Hydrophyllaceae, 205–216, 293–298, 449–465. *See also* Hydrophyllaceae
Chromosome numbers in Nicotiana, and morphology, 158, 345 ff.
Chromosome size in Crepis: decrease in, 242, 271, 273; relations of climate to changes in, 272; causes of decrease in, 272
Chromosomes in Crepis: question of breaks in, 270; primitive type, 271; advanced types, 271; somatic, 372; morphology of parent species, 373; length in interspecific hybrids, 373; identification of parental, 378; configurations in hybrids, 379–393; associations and frequencies of types, 386. *See also* Chromosome asymmetry; numbers, and size in Crepis; Crepis; Crepis hybrids
Chromosomes in Lilium longiflorum, 33–44; arrangement of "tassement polaire," 34
Chromosomes in Nicotiana: and cell metabolism, 2; types of Nicotiana Tabacum, 3–22; pairing, 157; morphology, 158–163, 347; behavior in species, 163–168, in hybrids, 168 ff.; insertion regions, 163 ff.
Colaconema. For index of species see p. 446
Conferva. For index of species see p. 446
Constance, Lincoln: **A Systematic Study of the Genus Eriophyllum Lag.**, 69–136; and Marion A. Cave, **Chromosome Numbers in the Hydrophyllaceae**, 205–216, 293–298, 449–464
Copeland, Edwin Bingham, **Filicum Novarum CXXVIII Diagnoses**, 217–226
Crepis: evolutionary processes in, 241, 273; chromosome numbers, 241, 243, 267–270, 273, 369–370, 389; polyploidy, 241; karyotype changes, 241, 273, 369 ff., 389; chromosome asymmetry, 242, 269, 273; decrease in chromosome size, 242; sections, 243–266; question of chromosome breaks in, 270–271; reciprocal translocations, 369; meiosis, 375
Crepis hybrids: somatic chromosomes, 372; chromosome length, 373; satellites, 373, 375; identification of parental chromosomes, 378; meiosis, 377; diakinesis, 378; chromosome configurations, 379–385; terminalization of chiasmata, 387, 388; inversion bridges, 388
Crepis Kotschyana, 258, 259, 269, 371–378 *passim*, 383, 385, 386, 389; origin, 391, 392, 393; translocations, 393

Crepis sections, karyotypes in, 243
  Anisorhamphus, 250
  Berinea, 253
  Brachypodes, 247
  Desiphylion, 244
  Gephyroides, 251
  Hostia, 257
  Intybellia, 255
  Ixeridopsis, 254
  Lepidoseris, 261
  Macropodes, 254
  Mesomeris, 247
  Mesophylion, 256
  Microcephalum, 259
  Nemauchenes, 263
  Omalocline, 245
  Paleya, 249
  Phaecasium, 256
  Phytodesia, 261
  Psammoseris, 266
  Pterotheca, 260
  Soyeria, 248
  Spathoides, 245
  Zacintha, 260
Crepis species, karyotypes of
  achyrophoroides, 263
  aculeata, 263, 265, 266
  albida, 249, 259, 260
  albiflora, 246, 247
  alpestris, 249, 250, 251, 253
  alpina, 257, 258, 259, 269
  amplexifolia, 263, 265, 266
  apula, 261, 262
  aspera, 263, 265, 266
  aurea, 246, 247, 249, 251, 259, 260
  auriculaefolia, 253
  Baldaccii, 252, 253
  bellidifolia, 265, 266
  biennis, 253, 261, 267
  bithynica, 254
  blattarioides, 248, 249, 250, 251, 253
  Bourgeauii, 261, 263
  Bungei, 254, 256, 257
  bursifolia, 265, 266
  canariensis, 263
  capillaris, 261, 262, 267, 270
  chondrilloides, 252, 253
  ciliata, 253, 267
  Clausonis, 263
  chrysantha, 246, 247, 256
  conyzaefolia, 248, 249, 253
  corymbosa, 261, 262
  cretica, 261, 262
  crocea, 254
  Dioscoridis, 260, 261
  divaricata, 263
  elegans, 255
  eritreënsis, 258, 259, 269
  flexuosa, 254, 255
  foetida, 257, 259, 269
    commutata, 258
    vulgaris, 258
  Fontiana, 261, 263
  fuliginosa, 261, 262, 268, 269, 270, 272
  geracioides, 244, 245
  gymnopus, 255, 256
  hierosolymitana, 247, 248
  hokkaidoensis, 246, 247, 256
  Hookeriana, 254
  hypochaeridea, 250
  incana, 252, 253
  incarnata, 255, 256
  Jacquini, 246, 247
  juvenalis, 263, 265, 266
  kashmirica, 245
  kilimandscharica, 250
  Kotschyana, 258, 259, 269
  lapsanoides, 247, 248
  latialis, 252, 253
  leontodontoides, 251, 253, 259, 260
  lybica, 261, 263
  lyrata, 247, 248
  Marschallii, 263
  mollis, 247, 248
  montana, 247, 248
  multicaulis, 258, 259, 260
  multiflora, 260, 261
  Mungierii, 247, 248
  nana, 254, 255
  neglecta, 261, 262, 268, 269, 270, 272
  Newii, 250
  nicaeënsis, 261, 262
  nigricans, 265, 266
  Noronhaea, 263
  oporinoides, 252, 253
  oreades, 254
  palaestina, 257
  paludosa, 244, 245
  pannonica, 252, 253
  parviflora, 261, 262
  patula, 260, 261
  polytricha, 246, 247
  pontana, 248, 249, 250, 251, 253
  praemorsa, 255, 256
  pterothecoides, 257
  pulchra, 257
  pygmaea, 245
  Raulini, 252, 253
  Reuteriana, 256, 257
  Robertioides, 254
  rubra, 257, 258, 269
  sancta, 260
    bifida, 260
    nemausensis, 260
  scaposa, 250
  Schachtii, 254

Crepis species (*Continued*)
  senecioides, 265, 266
  setosa, 263, 265, 266
  sibirica, 244, 245, 248, 250, 251
  Stojanovii, 257
  suberostris, 251, 253
  Suffreniana, 261, 262
  suffruticosa, 250
  syriaca, 257, 258, 259, 269
  taygetica, 253, 267
  tectorum, 256, 257, 268
  terglouensis, 246, 247
  tingitana, 251, 253
  Thomsonii, 258, 259, 269
  Triasii, 252, 253
  vesicaria, 261, 263
    andryaloides, 264
    hyemalis, 264
    myriocephala, 264
    stellata, 264
    taraxacifolia, 264
    typica, 264
  viscidula, 244, 245, 247
  willemetioides, 247, 248
  Zacintha, 260, 261
Crepis species excluded, 227 ff.
  bulbosa, 237
  distincta, 233
  racemifera, 229
  rapunculoides, 229
  serawschanica, 233
  setigera, 229
Ctenopteris beleensis, 225
  bipinnata, 225
  bipinnatifidae, 225
  Brassii, 225
  celebicae, 225
  Clemensiae, 225
  fusca, 225
  integripaleata, 225
  Ledermanni, 225
  polytricha, 225
  pubipes, 225
  rawlinsonensis, 225
  rhodocarpa, 225
  schizophlebia, 225
  sesquipinnata, 225
  stellatosetosa, 225
  venulosoides, 225
Cyathea bidentata, 218
  cheilanthoides, 219
  costalisora, 218
  everta, 218
  globosora, 218
  gracillima, 219
  horridula, 219
  magna, 218
  melanacantha, 219
  pachyrrhachis, 218
  parva, 219
  pilulifera, 219
  pulcherrima, 219
  quadripinnatifida, 218
  tomentosissima, 219
Cyclophorus Brassii, 226
Cytology: definition, 1; cell metabolism in Nicotiana Tabacum, 1–22; structure of living matter, 1; metabolic changes, 1; vacuolar solution, 2; death of cell, 2; respiration, 2; arrangement of cell constituents, 2; relation of metabolism to chromosomal constitution, 2–22; physiological activity, 2; of cells from green leaves, 6–7; application of Altmann technique to plant, 23–32; reaction to freezing, 25–26, 33; fixed minerals, 33; Botanical Garden experiments, 33
Cytoplasm: living, unstainable, 1, 3; proper killing of, 1; lipo-proteid, 2; contact with vacuolar solution, 2, 6; building of normal, 6; metabolic activity, 2, 17, 2; fixation in freezing-drying technique, 23, 25, 38; differentiation of chromatin from, 24; line of demarcation between nucleus and, 26

Dennstaedtia magnifica, 218
Diakinesis: in Lilium longiflorum, 37; in Nicotiana of Alata-group, 163–168 *passim;* chiasmata in Crepis and hybrids, 376; in interspecific Crepis hybrids, 378
Dicksonia Archboldii, 217
Dicranopteris tomentosa, 217
Digitalis purpurea, 139
Dislocation hypotheis, 268, 269, 369, 389
Drosophila, 37, 373
Dryopteris adenostegia, 220
  albosetosa, 221
  belensis, 220
  crassa, 220
  deltiptera, 220
  distincta, 220
  habbemensis, 219
  morobensis, 221
  multiauriculata, 221
  ophiura, 220
  paripinnata, 220
  petrophila, 220
  platyptera, 219
  protecta, 221
  pulchra, 219
  Regis, 220
  riparia, 221
  speciosissima, 219
  spinosa, 219
  strigosissima, 221

  subappendiculata, 220
  subdimorpha, 220
  terrestris, 221
  vestigiata, 220
  wantotensis, 220
Dufrenoy, J., **Comparative Metabolism of the Cells of Various Chromosomal Types of Nicotiana Tabacum**, 1–22

Egletes Californicus, 89, 91
Elaphoglossum Archboldii, 226
  brunneum, 226
  fuscum, 226
  habbemense, 226
  laticuneatum, 226
  repens, 226
Emmenanthe, chromosome numbers in, 209, 212, 213
Eremonanus, 71
Eriophyllum: systematic study of, 69–136; historical introduction to, 69; phyletic tendencies within, 72, 73; geographical distribution, 74–78; center of dispersal, 74; on Guadalupe Island, 76, 91; geological record, 78; taxonomic treatment, 79–135; original and amplified description, 79; key to species, 80; plants of possible hybrid origin, 111; species of, excluded, 121
Eriophyllum, 69–72, 79–81 *passim*
  absinthifolium, 121
  achillaeoides, 87
  alternifolium, 121
  ambiguum, 72, 73, 80, 116, 117
  ambrosioides, 121
  anthemoides, 121
  arachnoideum, 91
  artemisiaefolium, 112
  aureum, 118, 119
  bahiaefolium, 121
  Bigelovii, 121
  biternatum, 106, 108, 121
  Bolanderi, 96, 97
  brachylepis, 104
  Brownii, 91, 92
  caespitosum, 69, 83, 84, 91, 92, 94, pl. 3
    var. achillaeoides, 87
    var. grandiflorum, 89
    var. integrifolium, 94, 96, 97, 100, 102, 104
    var. latifolium, 91, 92
    var. leucophyllum, 97, 101
  cheiranthoides, 106, 108
  chrysanthemoides, 121
  chrysanthum, 96
  cineraria, 96
  confertiflorum, 72, 73, 93, 104, 106, 108, 110, 111, 112, 114
    var. discoideum, 106, 109
    var. latum, 106, 109
    var. laxiflorum, 106, 108, 109
    var. tanacetiflorum, 110–111
    var. trifidum, 106, 108, 109
  Congdoni, 115, 116
  croceum, 93
  crucigerum, 106, 108
  cuneatum, 90, 96
  Cusickii, 87, 88
  cuneatum, 90, 96
  gracile, 97, 101
  grandiflorum, 89
  Greenei, 87, 88
  Harfordii, 83, 85
  Heermannii, 121
  idoneum, 87
  Jepsonii, 106
  lanatum, 72, 74, 76, 81–92, 95, 97, 98, 104, 105, 106, 109, 114
    var. achillaeoides, 72, 76, 81, 87–93, 96, 105
    var. croceum, 92–96 *passim*
    var. cuneatum, 94, 96
    var. grandiflorum, 72, 89–91, 93, 96
    var. Hallii, 94–96, figs. 5–14, pl. 5
    var. integrifolium, 73, 85, 86, 96, 97, 99, 100–105
    var. lanceolatum, 104, 105–106
    var. leucophyllum, 83
    var. monoense, 97, 102
    var. obovatum, 104, 105, 112
    var. typicum, 83, 85, 86, 88, 89, 92, 99, 101
  lanceolatum, 105
  lanosum, 73, 117–118
  latilobum, 93, 106, 111–112
  leucophyllum, 97, 101
  lutescens, 97, 102
  minus, 121
  mohavense, 121
  monoense, 97, 102
  multicaule, 73, 76, 120
  multiflorum, 97, 100
  neomexicanum, 121
  nevadense, 97, 100, 102
  Nevinii, 72, 114
  nubigenum, 72, 115, 116
    var. **Congdoni**, 115–116
  nudicaule, 121
  oblongifolium, 121
  obovatum, 104
  oppositifolium, 121
  paleaceum, 116, 117
  Parishii, 116, 117
  parviflorum, 116, 117
  pedatum, 121
  pedunculatum, 83, 85

Eriophyllum (*Continued*)
  Pringlei, 73, 120
  resinosum, 121
  Rixfordii, 105
  sinuata, 121
  speciosum, 89, 90
  staechadifolium, 69, 72, 109, 112, 113, 114
    var. artemisiaefolium, 112
    var. depressum, 112, 113
  superbum, 83, 85
  tanacetiflorum, 110
  tenuifolium, 106, 108
  ternatum, 87, 88
  trichocarpum, 97, 100, 102
  tridactylum, 106, 108
  trifidum, 106, 108
  trollifolium, 69, 91, 92
  Wallacei, 73, 118
    var. calvescens, 118, 119
    var. rubella, 118, 119
  Watsonii, 97, 102
  Woodhousii, 121
Eubank, Lois L., **Hawaiian Representatives of the Genus Caulerpa, 409–432**
Eucrypta, chromosomes and chromosome numbers, 207, 210, 211, 293
  chrysanthemifolia, 296, 297, 298
    var. bipinnatifida, 296, 297, 298
Evolution, karyotype, 369 ff.

Ferns, New Guinea, 217
Freezing process: character and rate of, 25; significance of reactions of plant cells, 26, 33

? Galinsoga resinosa, 121
Gene(s): control physiological activity of plant cells, 2; division, 36, 37; "gene strings" in Lilium longiflorum, 37; mutation in species differentiation, 156; pairing of chromosomes with similar, 157
Gigantism in Nicotiana. *See* Nicotiana, Australasian species
Goniophlebium subcordatum, 226
  subimpressum, 226
Goodspeed, T. H.: **Three New Species of Nicotiana from Peru, 137–152; A Fourth New Species of Nicotiana from Peru, 195–204; Studies in Nicotiana. III. A Taxonomic Organization of the Genus, 335–344; Chromosome Number and Morphology in Nicotiana. VII. Karyotypes of Fifty-five Species in Relation to a Taxonomic Revision of the Genus, 345–368**; and F. M. Uber, **Application of the Altmann Freezing-Drying Technique to Plant Cytology. II. Character of the Fixation, 23–32**; F. M. Uber, and P. Avery, **Chromosome Structure in Lilium longiflorum, 33–44**
Grammitis brevisetulosa, 223
  caricifolia, 223
  ceratocarpa, 223
  cyclosora, 224
  debilifolia, 223
  dictymiodes, 223
  dorsipilae, 224
  Fenicis, 224
  frigidae, 223
  graminifolia, 223
  habbemensis, 223
  hirtellae, 224
  hispida, 224
  Holttumii, 224
  insularis, 223
  knutsfordianae, 224
  locellatae, 223
  loculosae, 223
  Mariae, 223
  marivelesensis, 224
  matapensis, 223
  mollipilae, 224
  Myer-Dreesii, 223
  neocaledonica, 222
  nigropaleata, 224
  nigrosetosa, 224
  novoguineensis, 223
  nudicarpa, 222
  peninsularis, 224
  plurisetulosa, 223
  scabristipedi, 223
  stomatocarpa, 223
  Stresemannii, 224
  trichopodae, 224
  trogophylla, 224
Grania efflorescens, 438

Helenium, 69, 71, 79
  caespitosum, 83
  lanatum, 83
  staechadifolium, 112
  trollifolium, 91
Hicriopteris Clemensiae, 217
Hydrolea, chromosome numbers in, 206
Hydrophyllaceae, chromosome numbers in, 205–216, 293–298, 449–465
  Draperia, 452, 462
  Ellisia, 450, 452, 462
  Emmenanthe, 209, 212, 213
  Eriodictyon, 450, 451, 460, 464
  Eucrypta, 207, 210, 211, 298
  Hydrolea, 206
  Hydrophyllum, 206, 207, 210, 211
  Militzia, 250, 260, 264

  Nama, 250, 251, 260
  Nemophila, 206, 207, 210, 211, 452, 462
  Phacelia, 206, 208, 209, 212, 213, 214, 215, 294, 296, 298, 449, 450, 452, 454, 456, 458, 462–464
  Pholistoma, 206, 207, 210, 211, 452, 462
  Romanzoffia, 209, 212, 213, 458, 464
  Turricula, 450, 460, 464
  Wigandia, 206, 460, 464
Hydrophyllum, chromosome numbers in, 206, 207, 210, 211
Hypolepis Archboldii, 218

Inversion bridges, in Crepis hybrids, 388

Jenkins, J. A., and E. B. Babcock, **Chromosomes and Phylogeny in Crepis, 241–292**

Karyotype: defined, 241 n. 1; changes in Crepis, 241, 243; in Crepis sections, 243–266; in Crepis species, 243 ff.; general trends in, evolution, 273, 369 ff., 389. *See also* Crepis sections, karyotypes in; Crepis species, karyotypes of
Kylinia. For index of species see p. 446

Lasthenia (Monolopia) ambigua, 116, 117
Lepidocaulon caudatum, 218
Lilium longiflorum: anthers, 25; chromosome structure, 33–44
Lindsaya furcata, 218
Literature cited on: Cell Metabolism in Nicotiana Tabacum, 22; Altmann Technique. II, 28; III, 39; Studies in Nicotiana. II. A Taxonomic Survey of the Australasian Species, 67; The Genus Eriophyllum Lag., 122; Nicotiana Phylesis in the Alata-Group, 192; A Fourth New Species of Nicotiana from Peru, 198; Chromosome Numbers in the Hydrophyllaceae, 216, 465; Chromosomes and Phylogeny in Crepis, 289; Acrochaetium-Rhodochorton Complex, 330, 441; Taxonomic Organization of Nicotiana, 343; Karyotypes of Fifty-five Species of Nicotiana, 366; Karyotype Evolution in Crepis, 394; Hawaiian Representatives of Caulerpa, 424
Lomogramma angustipinna, 222

Malaspina Expedition, 69
Meiosis: relation to mitosis, 33, 37; in Crepis species, 375; in interspecific hybrids, 377
Meringium laxum, 217
Merinthosorus Hieronymi, 226
  Thomsoni, 226
Metabolism, cell, in Nicotiana Tabacum, 1–22
Mitochondria, 2; building of cytoplasm with normal, 6; inactive, 6; active, 6, 10; differentiate into plastids, 6, 8; influence of size on plastids, 7; differentiation into active chloroplasts, 8; rod-shaped nonsecreting, 8, 17; differentiation of, into starch-storing amyloplasts, 9, 10, 17; of liver cells, 10; of shaded leaves, 17
Mitosis: relation of meiosis to, 33, 37; in Lilium longiflorum, 36, 37; characteristic of, 38

Navashin, M.: dislocation hypothesis, 268, 369, 389, and essential correctness of, 269; initiated terminology for Crepis, 372; differential amphiplasty, 373; satellite behavior, 375; reciprocal translocations, 369, 386
Nemophila, chromosome numbers in, 206, 207, 210, 211, 452, 462
Nicotiana: cell metabolism in N. Tabacum, 1–22; heritable characters, 17; species from Peru, 137–139, 195–198; haploid chromosome number in, 153; from seed, 154; chromosome number and morphology, 158–163, 345–368; tomentosa group, 197; taxonomic organization, 336 ff.
Nicotiana, Alata-group: phylesis in, 153–194; 9- and 10-paired, 153; a phylogenetic unit, 153, 190; center of distribution, 153; chromosome behavior in species, 163–168, and in hybrids, 168–184; F_1 hybrids, 168 ff.
Nicotiana, Australasian species: distribution, 45; chromosome number, 45–46; gigantism, 46, 60; value of cytogenetic data in classification, 46; tetraploidy, 46, 60–61, 65; special morphology of, 47 f.; key to, 49; descriptions, 49 ff.; doubtful species, 65 ff.; index to, 68
Nicotiana suaveolens, 45 f., 46, 56; distinguished from other species, 50–65 *passim;* odor compared, 55, 57, 63; described, 57–61
Nicotiana subgenera
  Rustica, 335, 336–337, 345, 348
  Tabacum, 1–22, 335, 337–339, 347, 348
  Petunioides, 335, 339–342, 345, 348–349
Nicotiana, taxonomic classification
  acaulis, 346, 349
  acuminata, 45, 346
  affinis, 154, 155
  alata, 153–182 *passim*, 186, 188, 189, 346, 348

- Nicotiana (*Continued*)
  - anisandra, 65
  - arentsii, 346
  - attenuata, 346, 349
  - Australasiae, 58, 59
  - australis, 65
  - **Benavidessi,** 137–138, 346, 348
  - Benthamiana, 49–50, 346, 349
  - bigelovii, 346
  - bonariensis, 153–158 *passim*, 162–168 *passim*, 174–179 *passim*, 346, 348
  - brasiliensis, 154
  - clevelandii, 346
  - commutata, 155
  - cordifolia, 346, 348
  - corymbosa, 346, 349
  - Debneyi, 51–52, 66, 346, 349
  - decurrens, 154, 155
  - excelsior, 50, 54, 346
  - **exigua,** 51, 52, 64–65, 66, 346, 349
  - fastigiata, 62 f., 65
  - flexuosa, 154
  - Forgetiana, 155, 188
  - Forsteri, 65
  - fragrans, 52, 66, 346, 349
  - fruticosa, 65
  - glauca, 346, 348
  - glutinosa, 346, 348
  - **Goodspeedii,** 62, 63–64, 65, 66, 346
  - Gossei, 50, 53–54, 57, 346, 349
  - ingulba, 50, 61–62
  - **Knightiana,** 139–140
  - Langsdorffi, 153–158 *passim*, 161–182 *passim*, 186, 188, 189, 346, 348
    - var. grandiflora, 155
  - linearis, 346, 349
  - longiflora, 153–158 *passim*, 160, 161, 163, 167, 168, 179, 180, 182, 187–190, 346, 348
    - var. acutiflora, 154
    - var. breviflora, 154
    - var. pauciflora, 154
    - var. oligantha, 154
  - Macgillivrayi, 52
  - macrocalyx, 50
  - **maritima,** 54 f., 56–57, 346
  - megalosiphon, 52, 54–55, 62, 346, 349
  - meirsii, 346, 349
  - mirabiliflora, 65
  - Neesii, 65
  - nesophila, 346
  - noctiflora, 346, 349
  - nudicaulis, 346, 349
  - **occidentalis,** 52–53, 346, 349
  - otophora, 197, 346
  - palmeri, 346
  - paniculata, 346
  - pauciflora, 346
  - persica, 154
  - petunioides, 346
  - plumbaginifolia, 153–158 *passim*, 160, 161, 346
  - pseudo-decurrens, 155
  - raimondii, 346
  - repanda, 346
  - rosulata, 62
  - rotundifolia, 61, 62–63, 64, 65, 346
  - rustica, 346
  - Sanderae, 155, 190, 346
  - **Setchellii,** 195–198 *passim*, 346, 348
  - solanifolia, 346, 348
  - spatulata, 154
  - spegazzinii, 349
  - **stenocarpa,** 61
  - **suaveolens,** 45, 46, 50–65 *passim*, 346, 349
    - var. anisandra, 65
    - var. cordifolia, 49, 50
    - var. Debneyi, 51, 65
    - var. excelsior, 50
    - var. longiflora, 54
    - var. macrantha, 52
    - var. parviflora, 51, 56, 66
    - var. rosulata, 62
    - var. rotundifolia, 62
    - var. tuberosa, 52, 66
    - var. undulata, 58, 59 f.
    - var. vincaeflora, 58, 59
  - sylvestris, 346, 348
  - tabacum, 346
  - **thyrsiflora,** 138–139, 346
  - tomentosa, 155, 197, 198, 346, 348
  - tomentosiformis, 197, 346, 348
  - trigonophylla, 346, 348
  - tristis, 154
  - undulata, 57 f., 58, 59 f., 346
  - **velutina,** 55–56, 57, 66, 346, 349
  - vincaeflora, 58, 59
  - wigandioides, 346
- Nierembergia, 65, 346

- **Oleandropsis,** 226
  - **ferrea,** 226
- **Orthiopteris cicutarioides,** 217
  - **trichophylla,** 217

- Paesia laevis, 218
- Papenfuss, George F.: **Review of the Acrochaetium-Rhodochorton Complex of the Red Algae,** 299–334; **Further Contributions Toward an Understanding of the Acrochaetium-Rhodochorton Complex of the Red Algae,** 433–448
- Petunia, 65
  - axillaris, 65
- Phacelia, chromosomes in sections
  - Cosmanthus, 462

  Euphacelia, 208, 298, 463
  Eutoca, 209, 298, 463
  Gymnobythus, 298, 462
  Microgenetes, 209, 293, 450, 463
  Whitlavia, 208, 298, 462
Phacelia: chromosome numbers in species, 205–216 *passim*, 293–298 *passim*, 449–465 *passim*
  affinis, 458, 463
  ammonphila, 208
  arizonica, 454, 463
  Bolanderi, 294, 298
  brachyloba, 296, 298
  Breweri, 208
  campanularia, 206, 454, 462
  cicutaria, 294, 298, 454, 463
    var. Hubbyi, 463
  ciliata, 206, 208
  circinata, 206
  coerulea, 454, 463
  Congdoni, 458, 463
  congesta, 206, 294, 298, 454, 463
  Cooperae, 458, 463
  crenulata, 294, 298
  cryptantha, 294, 298
  Davidsonii, 294, 298, 449
  distans, 208
    australis, 208
  divaricata, 206, 209
  dubia, 452, 462
  Eisenii, 456, 463
  eximia, 208
  Fremontii, 296, 298
  grandiflora, 294, 298
  hirsuta, 452, 462
  humilis, 456, 463
  hydrophylloides, 456, 463
  insularis, 463
    var. continentis, 458, 463
  Lemmoni, 293, 294, 298, 449, 458, 463
  linearis, 294, 298
  longipes, 294, 298
  magellanica-californica-heterophylla complex, 208–209, 214, 298, 463
    argentea, 208
    californica, 208, 298
      var. jacintensis, 209
    compacta, 208, 463
    frigida, 463
    heterophylla, 208
    imbricata, 208, 296, 298
    leucophylla, 209, 298
    mutabilis, 209, 456, 463
    nemoralis, 209, 298, 454, 463
    urticacea, 456, 463
    virgata, 296, 298
      var. bernardina, 296, 298
  minor, 206, 208
  mohavensis, 209
  neglecta, 458, 463
  Palmeri var. foetida, 294, 298
  Parryi, 206, 454, 462
  pedicellata, 294, 298
  phacelioides, 258, 263
  platycarpa, 452, 462
  Popei, 294
  pratensis, 449, 456, 463
  procera, 209
  Pringlei, 458, 463
  Purpusii, 458, 463
  Purshii, 452, 462
  Quickii, 456, 463
  racemosa, 456, 463
  ramosissima, 294, 449, 454, 463
  ranunculacea, 452, 462
  Rattani, 454, 463
  sericea, 209
  suffrutescens, 449, 454, 463
  tanacetifolia, 206
  vallicola, 458, 463
  verna, 294, 298
  viscida, 206, 452, 462
Phialis, 69, 79
Pholistoma, chromosome numbers in, 206, 207, 210, 211
Phylogenetic decrease in chromosome numbers, 268; Tobgy's demonstration, 268, 269
Plastids, 2; size, 3, 6–7, 17; mitochondria differentiated into, 6, 8; influence of size of mitochondria on, 7; starch content, 11, 14, 15; devoid of starch, 17; lipo-proteidic substance, 17 f.
Pleonosporium constrictum, 329
Pollen: monosomic types of Nicotiana Tabacum, 3; vital staining, 3, 5
Polyploidy: in Phacelia, 206; in Crepis, 241
Polypodium crassimarginatum, 226
Polystichum Archboldii, 221
  cheilanthoides, 221
  muticum, 221
  Myer-Dreesii, 221
Prosaptia Archboldii, 226
Pteris macrophylla, 218

Reticulum: chromatin granules, 35; resting, 35
Rhodochorton. For index of species, see pp. 446–447
Romanzoffia, chromosome numbers in, 209, 212, 213

Selliguea brachylepidota, 226
Sequoia gigantea, 94
  sempervirens, 94

Sherman, Marta, **Karyotype Evolution: A Cytogenetic Study of Seven Species and Six Interspecific Hybrids of Crepis**, 369–408
Somatic tissue: irregular distribution of nuclear material in, of Nicotiana Tabacum hybrids, 20–21; resting nuclei of frozen-dried mammalian, 35
Spermothamnion, speluncarum, 329
Starch metabolism, 8 ff.; translocation controlled by temperature, 9; storage of grains, 9; premature storage, 10; secretion by chondriome cause of, 10–11; inhibition of translocation, 14–15; effect of darkness on utilization and translocation, 15, 17
Stebbins, G. L., Jr., and E. B. Babcock, **Systematic Studies in the Cichorieae**, 227–240
Structural sequence, mitotic, 38
Syntrichopappus, 71

Tectaria pubescens, 221
Tetraploidy in Nicotiana. *See* Nicotiana, Australasian species
Thamnidium. For index of species see p. 447
Tobgy, H. A., cited on: decrease in chromosome numbers, 268–269, 370; chromosome length, 377; chains of chromosomes in Crepis, 386
Tomentosa group in Nicotiana, 197
Tradescantia, chromosome tract, 34
Translocation of carbohydrates. *See* Starch metabolism
Translocations, reciprocal, in Crepis: and changes in chromosome number, 268, 369; and increase in asymmetry, 269; opposing tendencies, 270; origin, 383, 385; apparent absence, 385; in C. Kotschyana, 393.
Trichophyllum, 69, 70, 79
  integrifolium, 96–102 *passim*, pl. 6
  lanatum, 69, 83
  multiflorum, 97, 99, 100, 101, pl. 7
Triticum, 373

Uber, F. M., and T. H. Goodspeed: **Application of the Altmann Freezing-Drying Technique to Plant Cytology. II. Character of the Fixation**, 23–32; and Priscilla Avery, **III. Chromosome Structure in Lilium longiflorum**, 33–44
University of California Botanical Garden: investigations in cytogenetics and experimental cytology, 33; expeditions to the Andes, 137, 138, 195; Nicotiana in, 138, 140, 154, 198

Vacuolar solution, 1, 2, 3; total flocculation, 2; complex precipitates, 2; cytoplasm in contact with surface of, 2; accumulation of amino acids, 2, 17; staining, 3; instability, 3

Wheeler, Helen-Mar, **Studies in Nicotiana. II. A Taxonomic Survey of the Australasian Species**, 45–68
Wigandia, chromosome numbers in, 206

Xithopteris antipodalis, 224

Youngia, relationships of
  distincta, 233–235
  racemifera, 229–231
  serawschanica, 231–233
  setigera, 227–229

Zea, 386
  mays, 3

ERRATA

Page 56, between lines 11 and 12. *Insert a paragraph, as follows:* Distinguishable from *N. suaveolens* by dense, velvety, more or less viscid indument, petiole, smaller flower. Closely related to *N. maritima,* from which distinguishable by indument, petiole.

Page 210, line 8. *For* I A, I T, I A *read* I T, I A, I T

Page 212, line 3. *For* Diak. *read* Interk.

Page 212, line 9. *For* I T *read* I I T

Page 220, line 30. *For* glandilis *read* glandulis

Page 221, line 44. *For* forman *read* formam

Page 222, line 9. *For* solictariis *read* solitariis

Page 224, line 29. *For* frevioribus *read* brevioribus

Page 252, fig. 10. *For* C. Raulinii *read* C. Raulini

Page 263, fig. 21. *For* C. lybrica *read* C. lybica

Page 302, line 15. For *inserte* read *incertae*

Page 311, line 5. *For* Acrocheatium *read* Acrochaetium

Page 312, line 41. *For* Bonne. *read* Bonne-

Page 313, line 38. *For* Chili *read* Chile

Page 320, line 35. *For* or *read* on

Page 330, line 34. *For* Clug *read* Club

Page 346, three right-hand columns of table 1. *Insert* N. Spegazzinii . . . 12 . . . Goodspeed, 1945*a*

Page 348, table 2, last column, figure reference, N. Thyrsiflora. *Omit* 1, *h*

Page 348, table 2. *For* N. rustica . . . 24 . . . 12 . . . 12^2 . . . 1, *i, read* N. rustica . . . 24 . . . 12 . . . 12^2 . . . 1, *h*

CONTENTS

PAGES

Comparative Metabolism of the Cells of Various Chromosomal Types of *Nicotiana Tabacum*, by J. Dufrenoy 1

Application of the Altmann Freezing-Drying Technique to Plant Cytology

II. Character of the Fixation, by T. H. Goodspeed and F. M. Uber 23

III. Chromosome Structure in *Lilium longiflorum*, by T. H. Goodspeed, F. M. Uber, and P. Avery 33

Studies in *Nicotiana*. II. A Taxonomic Survey of the Australasian Species, by Helen-Mar Wheeler 45

A Systematic Study of the Genus *Eriophyllum* Lag., by Lincoln Constance 69

Three New Species of *Nicotiana* from Peru, by T. H. Goodspeed 137

Cytogenetic Evidences of *Nicotiana* Phylesis in the Alata-Group, by Priscilla Avery ... 153

A Fourth New Species of *Nicotiana* from Peru, by T. H. Goodspeed 195

Chromosome Numbers in the Hydrophyllaceae, by Marion S. Cave and Lincoln Constance 205

Filicum Novarum CXXVIII Diagnoses, by Edwin Bingham Copeland 217

Systematic Studies in the Cichorieae, by E. B. Babcock and G. L. Stebbins, Jr. 227

Chromosomes and Phylogeny in *Crepis*. III. The Relationships of One Hundred and Thirteen Species, by E. B. Babcock and J. A. Jenkins 241

Chromosome Numbers in the Hydrophyllaceae: II, by Marion S. Cave and Lincoln Constance 293

Review of the *Acrochaetium-Rhodochorton* Complex of the Red Algae, by George F. Papenfuss 299

Studies in *Nicotiana*. III. A Taxonomic Organization of the Genus, by T. H. Goodspeed 335

Chromosome Number and Morphology in *Nicotiana*. VII. Karyotypes of Fifty-five Species in Relation to a Taxonomic Revision of the Genus, by T. H. Goodspeed 345

Karyotype Evolution: A Cytogenetic Study of Seven Species and Six Interspecific Hybrids of *Crepis*, by Marta Sherman 369

Hawaiian Representatives of the Genus *Caulerpa*, by Lois L. Eubank 409

Further Contributions Toward an Understanding of the *Acrochaetium-Rhodochorton* Complex of the Red Algae, by George F. Papenfuss 433

Chromosome Numbers in the Hydrophyllaceae: III, by Marion S. Cave and Lincoln Constance 449

Index 467